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Descriptions of New *Hypochilus* Species from New Mexico and California with a Cladistic Analysis of the Hypochilidae (Araneae)

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ABSTRACT

Two new species of the lampshade spider genus *Hypochilus* are described, *H. jemez* from New Mexico and *H. bernardino* from southern California. The species relationships of the genus are analyzed cladistically using comparative morphological data. The genus *Hypochilus*, as here construed, comprises ten species: *H. pococki*, *H. sheari*, *H. coylei*, *H. gertschi*, *H. thorelli*, *H. bonneti*, *H. jemez*, *H. petrunkevitchi*, *H. bernardino*, and *H. kastoni*. A cladogram is presented which supports the following phylogeny: 1) *H. bonneti* and its allopatric sister species *H. jemez*, both confined to the southern Rocky Mountains, are the most plesiomorphic clade and sister group to the Sierra

Nevada and Appalachian clades, 2) *H. petrunkevitchi*, *H. bernardino*, and *H. kastoni* comprise a Sierra Nevada clade with disjunct distributions in the Sierra Nevada, San Bernardino, and Cascade Mountains of California, and 3) *H. coylei*, *H. gertschi*, *H. thorelli*, *H. pococki*, and *H. sheari*, all found in the southern Appalachians, form the most apomorphic clade. A taxonomic key, table of quantitative character values, distribution maps, and notes on the distribution and natural history of *H. jemez* are presented, as is a discussion of the biogeographical implications of the putative relationships.

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INTRODUCTION

An early paper by Marx (1888), who first described the taxon, and later papers by Petrunkevitch (1932) and Gertsch (1958), recognized and reinforced the importance of *Hypochilus* Marx as a relict taxon at the base of the infraorder Araneomorphae (Platnick, 1977; Forster et al., 1987). Plesiomorphic characters of the Hypochilidae (*Hypochilus* and *Ectatosticta* Simon) include, among others, the retention of two pairs of book lungs, semidiaxial chelicerae, and venom glands restricted to the chelicerae (Gertsch, 1958); for others see Marples (1968), Platnick (1977), and Forster et al. (1987). Synapomorphies supporting the monophyly of the Hypochilidae include: serrula comprising several rows of teeth, no tarsal scopulae or claw tufts, male palpal bulb terminal, spine-bearing paracymbium (conspicuous stout macrosetae pressed closely together form essentially a single element) (Forster et al., 1987), cheliceral concavities, single coxal glands, spinneret segments reduced to 1 or 2 (Coddington, 1990), ringed spigot morphology (Platnick et al., 1991).

The genus *Hypochilus* was long believed to be monotypic, represented by *H. thorelli* Marx in the mountains of the southeastern United States. Gertsch (1958) described a second species, *H. petrunkevitchi* Gertsch, from the mountains of central California. Hoffman (1963a) described a second eastern species, *H. gertschi* Hoffman, from western Virginia, closely followed by Gertsch (1964), who described *H. bonneti* Gertsch, apparently confined to deep canyons in central Colorado. Platnick (in Forster et al., 1987) added three more species (*H. pococki* Platnick, *H. coylei* Platnick, and *H. sheari* Platnick) to the fauna of the southern Appalachians and *H. kastoni* Platnick from northern California. Two additional species, *H. jemez* from the Sangre de Cristo mountains of New Mexico and *H. bernardino* from the San Bernardino mountains of southern California are described in this paper, bringing the total of known species to ten.

The biology of these enigmatic spiders is not well known, being limited to studies by Marples (1968 on internal anatomy), Shear (1969 on predatory behavior in *H. gertschi*),

Fergusson (1972 on natural history of *H. pococki*), Foelix and Jung (1978 on morphology of *H. thorelli*), Riechert and Cady (1983 on community ecology of *H. thorelli*), Coyle (1985 on the life cycle of *H. pococki*), Alberti and Coyle (1991 on sperm morphology), Huff and Coyle (1992 on the systematics of *H. coylei* and *H. sheari*), Eberhard et al. (in press, mating systems in *H. pococki*), and Catley (1993, on reproductive biology of *H. pococki*).

Considering the phylogenetic significance of the family, as the sister group to all other araneomorph spiders, it is surprising that no analysis of relationships within the genus has been attempted. Apart from Hoffman (1963a), who commented on the similarity between *H. gertschi* and *H. petrunkevitchi*, no phylogenetic hypothesis has been erected.

METHODS

Drawings were made either with the aid of a drawing grid or camera lucida. Measurements were made with a Wild M-5 stereomicroscope and Wild M-20 compound microscope fitted with a Lasico digital micrometer or a 120-unit eyepiece micrometer determined to be accurate to 0.038 mm. Spermathecae were dissected from the relevant section of body wall, overlying tissue removed with needles, and then cleared in 85 percent lactic acid. Scanning electronmicrographs were made on Zeiss DSM 950 and JOEL 848 scanning electron microscopes.

Some characters chosen were discrete (number of cheliceral teeth) and others were morphometric (measurements and ratios of measurements). Great care was taken to ensure that morphometric characters did in fact define discrete characters and not traits. Any ambiguity in character definition resulted in the most conservative approach being taken. In order to detect quantitative characters which define clusters of species, data were plotted as bivariate scatterplots. Such characters which showed no overlap as well as nonquantitative characters which also clustered species, were selected for use in the cladistic analysis.

ABBREVIATIONS

Institutional

AMNH	American Museum of Natural History
CAS	California Academy of Sciences
MNHN	Muséum National d'Histoire Naturelle, Paris
USNM	National Museum of Natural History, Washington
WCU	Western Carolina University

Characters

AME	diameter of anterior median eye pupil
AMEi	minimum interdistance between anterior median eye pupils
APC	shape of apex of male palpal conductor (figs. 21–31)
CdL	male palpal conductor length in retrolateral view (fig. 3)
CTre	number of retromarginal cheliceral teeth (fig. 19)
CW	cephalothorax width
F1M	stout black macrosetae (with prominent folded bases) on the dorsal and prolateral proximal aspect of male femur 1 (fig. 20)
PCT	number of promarginal cheliceral teeth (fig. 19)
PMA	index of shape of male palpal median apophysis; vertical height of distal edge of apophysis $\times$ length of ventral border of apophysis (fig. 4)
PTW/PTL	maximum width of male pedipalpal tibia in retrolateral view/length of tibia in retrolateral view (fig. 1)
PTaL	length of male palpal tarsus in retrolateral view (fig. 3)
PTaM	black "thumbprint" mark on retrolateral surface of male pedipalpal tarsus (fig. 3)
SP	intensity of sternal pigmentation

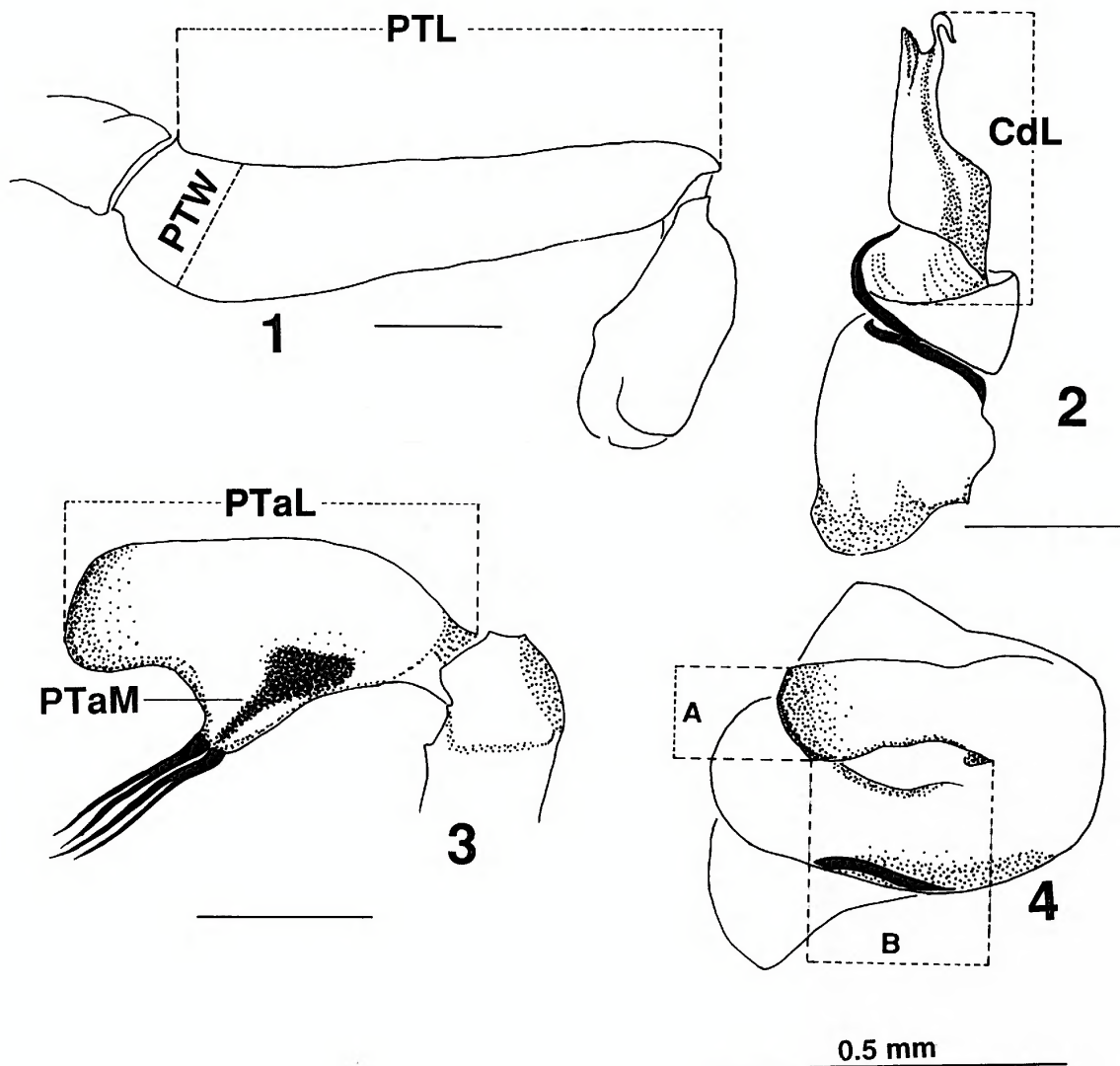
CLADISTIC ANALYSIS: Decisions concerning the evolutionary polarity of character transformations were based exclusively on outgroup comparison with *Ectatosticta davidi* Simon, the monotypic Chinese genus considered to be the sister taxon of *Hypochilus* (Forster et al., 1987). The resulting matrix of 11 taxa and 13 characters (table 2) was analyzed using the Hennig86 version 1.5 computer program (Farris, 1988) with the cladogram rooted at the outgroup. Preliminary analyses were achieved running the most par-

simonious Hennig86-derived trees on the interactive graphic software Clados 1.2 (Nixon, 1992) allowing alternative rootings, optimizations, and character evolution hypotheses to be tested. Statistical analysis was achieved using Statview II software (Abacus Concepts). Binary character states were treated as reversible. Multistate characters, where a transformation series could not be hypothesized a priori, were treated as unordered. However, I felt confident in ordering characters 5 (shape of male pedipalpal tibia) and 10 (number of promarginal cheliceral teeth). In an attempt to quantify the change in shape of the male pedipalpal tibia from the plesiomorphic condition (determined by outgroup comparison) of long and slender (fig. 5) to short and wide (fig. 6), a ratio of the maximum width divided by the maximum length was used as a character (fig. 1, table 1).

MATERIAL EXAMINED:

Hypochilus gertschi: **Virginia:** Buchanan Co.: Bear Wallow Mountain, rt. 613, 0.5 mi W junction with rt. 616, Aug. 19, 1977 (D. W. Ogle, AMNH) 4♂; rt. 83 just W Stacy, across Slate Creek, Aug. 29, 1977 (D. W. Ogle, AMNH) 2♂. **Bland Co.:** mouth of Hamilton's Cave, 4 mi E Mechanicsburg, Sept. 10, 1956 (R. L. Hoffman, AMNH) 1♀. **West Virginia:** Nicholas Co.: rt. 39, 1 mi W Swiss, Sept. 2, 1965, rock ledges (Brownell, R. L. Hoffman, AMNH) 1♀.

Hypochilus thorelli: **Alabama:** Cherokee Co.: Mary's Gulf, Sept. 1949 (A. F. Archer, AMNH) 1♀. **Madison Co.:** Hurricane Cave, 4 mi E New Market, Sept. 13, 1968 (S. B. Peck, AMNH) 1♀. **Marshall Co.:** 0.8 mi N Grant on Co. road 63, July 26, 1966 (F. A. Coyle, AMNH) 1♀. **Georgia:** Dade Co.: Boxcar Cave, Nov. 12, 1967 (T. Iles, AMNH) 1♀. **Kentucky:** Bell Co.: Pine Mountain, Aug. 12, 1919, elev. 2200 ft (671 m) (W. D. Funkhouser, AMNH) 1♂. **Whitley Co.:** Cumberland Falls State Park, Sept. 8, 1967 (Neff, R. L. Hoffman, AMNH) 1♂. **Tennessee:** Bell Co.: Chain Rock area, Pine Mountain State Park, June 30, 1967 (C. R. McGhee, AMNH) 1♀. **Hamilton Co.:** Signal Mountain, Aug. 30, 1969, elev. 1700 ft (518 m) (R. L. Hoffman, AMNH) 1♂. No data, 1♂ (AMNH). *Van Bu-*



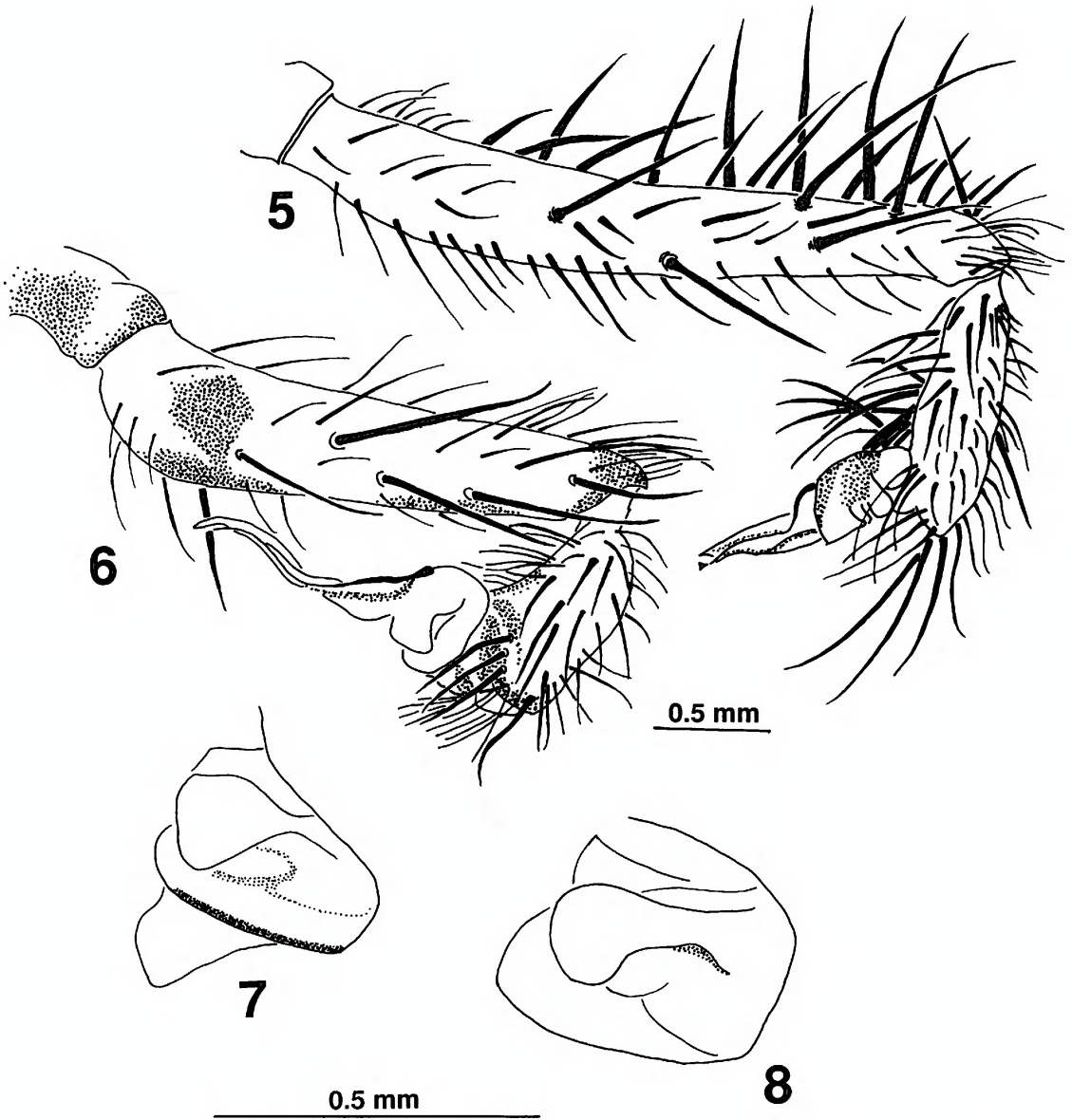
Figs. 1–4. 1. Male *H. gertschi*, left pedipalpal tibia, retrolateral view. 2. Male *H. bonneti*, palpal organ, retrolateral view. 3. Male *H. coylei*, left palpal organ, tarsus (= paracymbium), retrolateral view. 4. Male *H. sheari*, median apophysis of left palpal organ, A $\times$ B = PMA (all scale lines = 0.5 mm).

ren Co.: 1.5 mi E Spencer, Aug. 11, 1951 (AMNH) 1♂.

Hypochilus pococki: **Georgia**: Lumpkin Co.: Desoto Falls Recreation Area, rt. 19, July 30, 1966, elev. 2150 ft (655 m) (F. A. Coyle, AMNH) 1♂, 1♀. **North Carolina**: Jackson Co.: Wolf Creek, Cullowhee Mountain, July 1990, elev. 2800 ft (854 m) (author's personal coll.) 1♀; rocks along Tuckasegee River, Cullowhee, Oct. 1990, elev. 2600 ft (793 m) (B. Dellinger, author's personal coll.)

1♀. **Transylvania Co.**: ridge between White-water and Thomson River Gorges, Aug. 22, 1975, elev. 2800 ft (854 m) under ledge (D. Pittillo, AMNH). **Tennessee**: Blount Co.: The Sinks, Little River Gorge, Great Smoky Mountains National Park, Sept. 30, 1983, rock outcrops (F. A. Coyle, AMNH) 2♂, 1♀. **Sevier Co.**: Greenbrier Cove, 7–8 mi NE Gatlinburg, Oct. 2, 1960 (W. J. Gertsch, W. Ivie, AMNH) 1♂, 2♀.

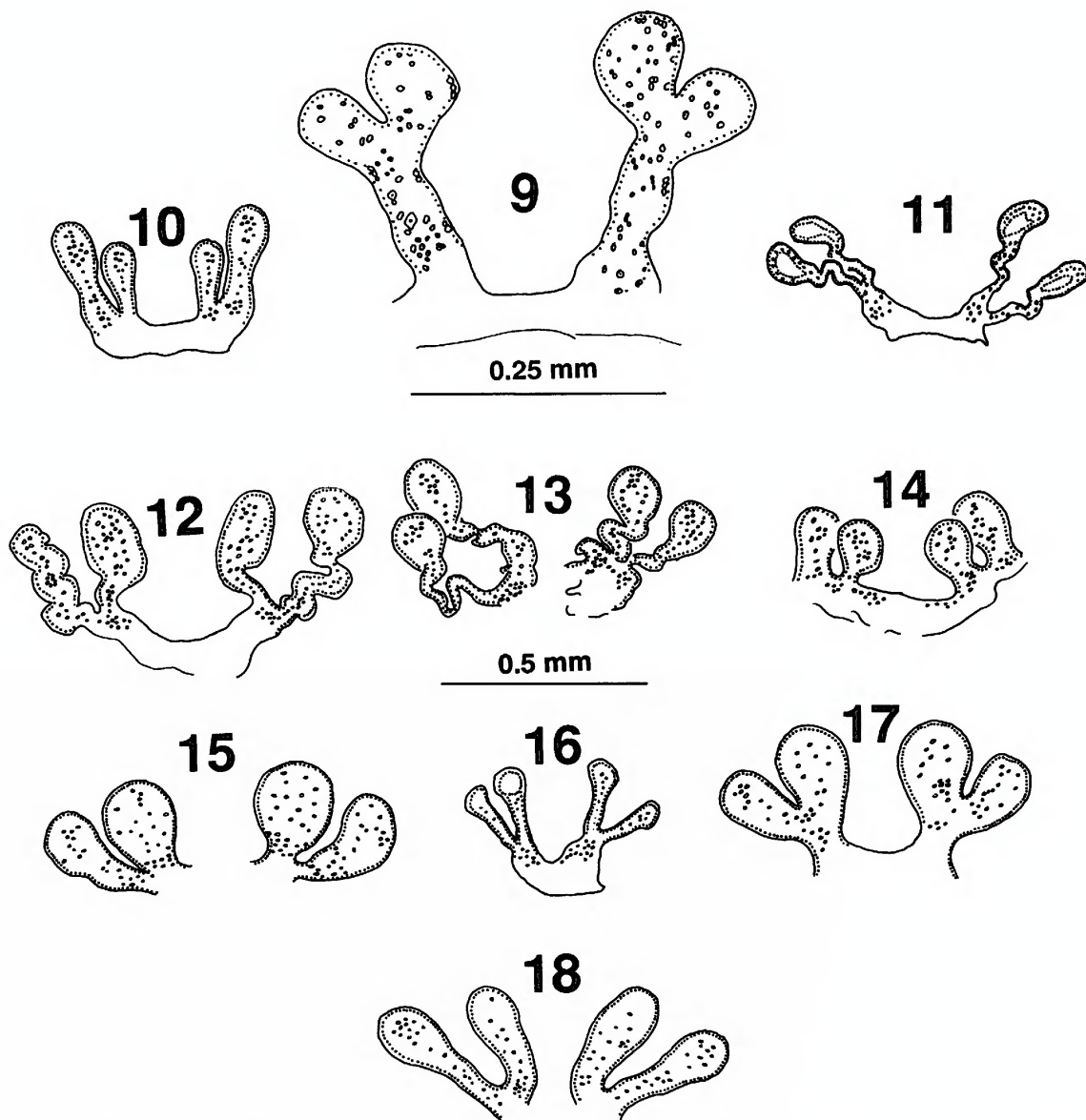
Hypochilus coylei: **North Carolina**: Hen-



Figs. 5–8. 5. Male *H. bonneti*, left pedipalp, prolateral view. 6. Male *H. gertschi*, left pedipalp, prolateral view. 7. Male *H. bernardino*, median apophysis of left palpal organ, prolateral view. 8. Male *H. petrunkevitchi*, median apophysis of left palpal organ, prolateral view.

derson Co.: Tusubreeches Creek, 1 mi SW of US 64, Oct. 3, 1987, elev. 2400 ft (732 m) rock outcrops above creek (R. P. Huff, WCU) 1♂, 1♀; Hickory Creek, 1 mi SE Gerton, Sept. 13, 1987, elev. 2575 ft (785 m) rock outcrops on both sides of road, deciduous forest (R. P. Huff, WCU) 1♀; Minihaha Falls, 0.8 mi N on NC9 from US74, Sept. 13, 1987, elev.

1600 ft (488 m) rock outcrop below road, mixed forest (R. P. Huff, WCU) 1♀. *Polk Co.*: Clifford Mountain, 2.5 mi W of Mountain View Church, Sept. 3, 1988 elev. 1300 ft (396 m) rock faces, dry hardwood forest, southern exposure (R. P. Huff, WCU) 1♂, 1♀. *Rutherford Co.*: Rainbow Falls, Rainbow Falls trail, 1.6 mi E of NC9 on US 74, Oct. 6, 1987,

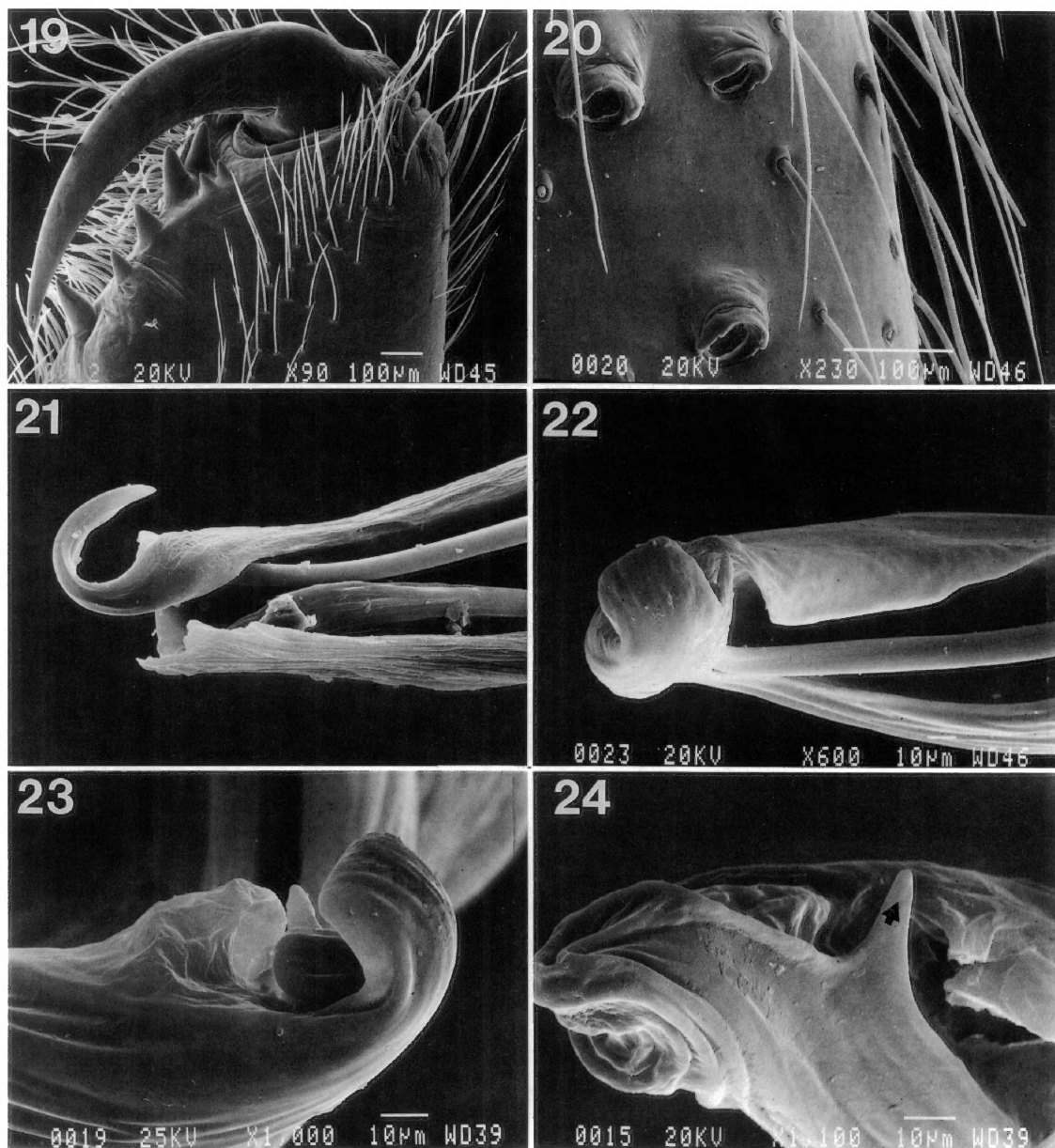


Figs. 9–18. Female spermathecae, dorsal view. 9. *H. jemez*, new species. 10. *H. kastoni*. 11. *H. bernardino*, new species. 12. *H. gertschi*. 13. *H. petrunkevitchi*. 14. *H. thorelli*. 15. *H. pococki*. 16. *H. bonneti*. 17. *H. sheari*. 18. *H. coylei*. 0.25 mm scale for fig. 9, 0.5 mm scale for all other figures.

elev. 1500–2200 ft (457–671 m) disturbed boulders along trail, fairly moist deciduous forest (R. P. Huff, WCU) 2♂; Broad River, 0.3 mi N Rainbow Falls trail, Sept. 3, 1988, elev. 1300 ft (396 m) disturbed rock on both sides of river (R. P. Huff, WCU) 1♀.

Hypochilus sheari. **North Carolina:** *Buncombe Co.*: Long Branch Creek, Long Branch Road 0.8 mi N Bee Tree Rd., Sept. 28, 1987, elev. 3100 ft (945 m) rock outcrop on right

of road (R. P. Huff, WCU) 1♂, 2♀; same locality, Oct. 15, 1988 (R. P. Huff, WCU) 1♂. *McDowell Co.*: Buck Creek, 9.9 mi N US 74 on NC 80, Sept. 1, 1987, elev. 3400 ft (1037 m) very dry exposed rock on right of SW exposure (R. P. Huff, WCU) 1♂, 1♀; Newburg Creek, 0.5 mi W on Newburg Creek from Curtis Creek confluence, Sept. 13, 1987, elev. 2400 ft (732 m) rock outcrops on both sides of road (R. P. Huff, WCU) 1♂; Mill Creek,

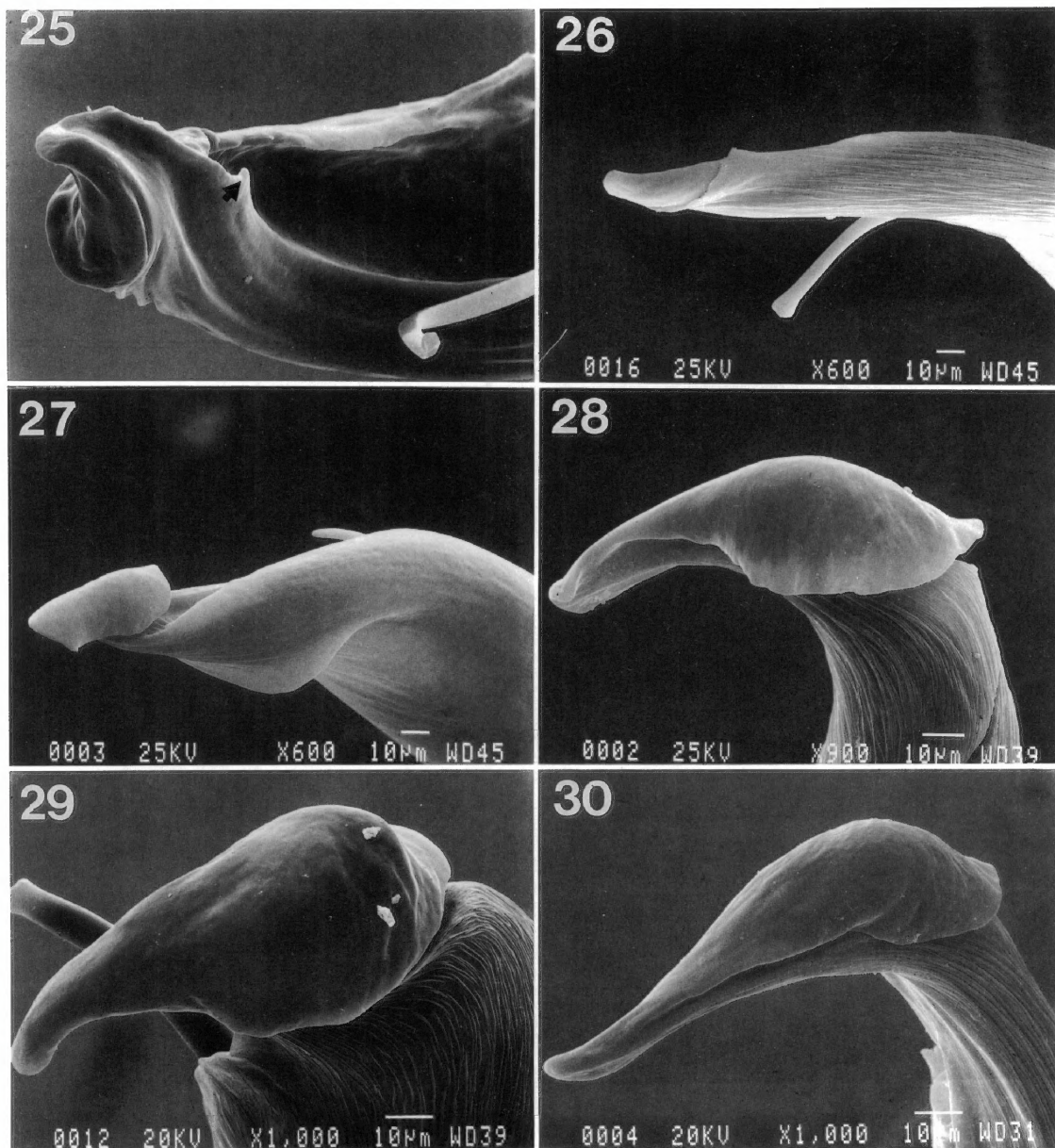


Figs. 19–24. 19. Male *H. coylei*, retromarginal cheliceral teeth (CTre). 20. Male *H. bonneti*, dorsal surface femur 1, bases of macrosetae (F1M). 21. Male *H. bonneti*, apex of palpal conductor (APC), 600 $\times$. 22. Male *H. kastoni*, apex of palpal conductor. 23. Male *H. kastoni*, apex of palpal conductor (APC). 24. Male *H. petrunkevitchi*, apex of palpal conductor (APC) arrow to distal conductor apophysis.

0.2 mi SE Andrews Geyser, Oct. 6, 1987, elev. 3100 ft (945 m) large rock outcrops on left, marginal dry habitat (R. P. Huff, WCU) 1♂, 1♀.

Hypochilus petrunkevitchi: **California:** *Fresno Co.*: Sheep Creek, Cedar grove, Kings Canyon, July, 16, 1952, elev. 4633–5200 ft

(1413–1586 m) (W. J. Gertsch, J. W. Gertsch, AMNH) 2♂. *Mariposa Co.*: base of Yosemite Falls, Yosemite National Park, Sept. 22, 1961 (W. J. Gertsch, W. Ivie, AMNH) 1♀. *Tulare Co.*: Belnap Springs, near Camp Nelson, Sequoia National Park, July 11, 1958 (W. J. Gertsch, V. Roth, AMNH) 1♂; S Giant Forest

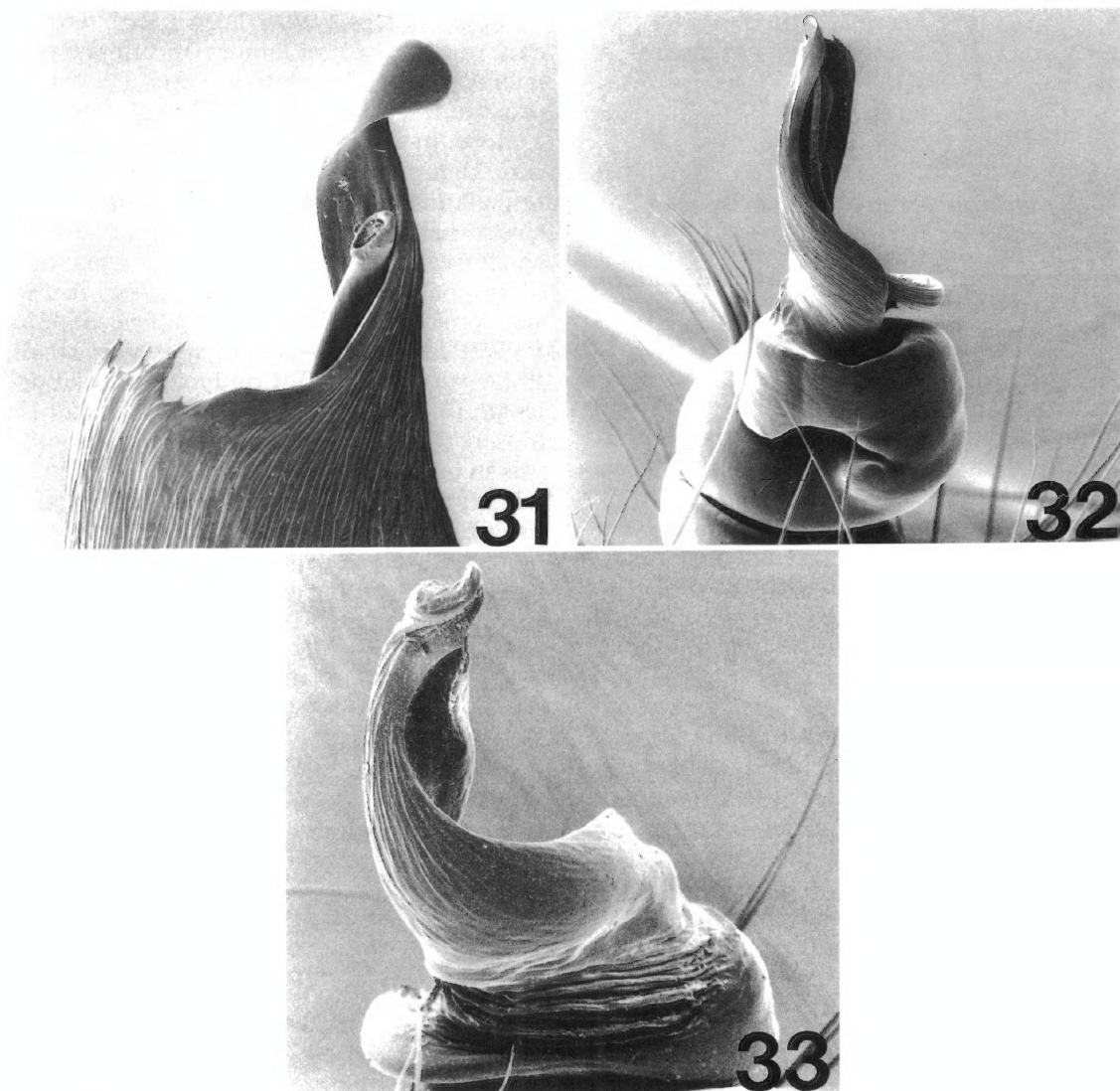


Figs. 25–30. 25. Male *H. bernardino*, new species, apex of palpal conductor, 700 $\times$ (APC) arrow to distal conductor apophysis. 26. Male *H. gertschi*, apex of palpal conductor (APC). 27. *H. pococki*, apex of palpal conductor (APC). 28. Male *H. thorelli*, apex of palpal conductor (APC). 29. Male *H. coylei*, apex of palpal conductor (APC). 30. Male *H. sheari*, apex of palpal conductor (APC).

Village, Sequoia National Park, Aug. 17, 1984, elev. 1800 m (T. S. Briggs, V. F. Lee, D. Ubick, CAS) 1♂.

Hypochilus bernardino (new species): See description below.

Hypochilus bonneti: **Colorado:** *Fremont Co.*: Fly Cave, Oil Creek, 13 mi N Canon City, April 28, 1961 (T. P. Maslin, C. J. McCoy, Jr., B. Vogel, AMNH) 1♂. *Gunnison Co.*: East Portal, Black Canyon National Monu-



Figs. 31–33. 31. Male *H. jemez*, new species, apex of palpal conductor, 725 $\times$ (APC). 32. Male *H. jemez*, palpal bulb, prolateral view, 139 $\times$. 33. Male *H. bernardino*, new species, palpal conductor, retrolateral view, 180 $\times$.

ment, July 26, 1962, elev. 6547 ft (1997 m) (B. Vogel, W. J. Gertsch, R. Graham, AMNH) 3 δ , 2 f .

Hypochilus jemez (new species): See description below.

Hypochilus kastoni: **California:** *Humboldt Co.*: beside Hwy 96, 4.2 mi S Somes Bar, Oct. 2, 1979, elev. 4500 ft (1372 m) in webs above stream on ceiling of upstream end of

6 ft diameter steel conduit under road (W. R. Icenogle, AMNH) 1 δ , 7 imm. *Siskiyou Co.*: 5 mi W Mount Shasta, Sept. 14, 1985 (W. C. Sedgwick, AMNH) 1 male holotype, female paratype; type locality, Sept. 2, 1959 (W. J. Gertsch, V. Roth, AMNH) 1 δ .

Ectatosticta davidi: **CHINA:** *Huangyuan County, Qinghai Province*: Sept. 10, 1983 (Li Zhong Shan, AMNH courtesy of Dr. D. Song)

1♂, 1♀; *Shaanxi Province*: "Inkiaphou" (donated to W. J. Gertsch by authorities at MNHN, AMNH) 1♀.

SYSTEMATICS

Hypochilus bernardino, new species

Figures 7, 11, 25, 33, 36–39

Hypochilus petrunkevitchi (misidentification): Forster et al. (1987): p. 22 (San Bernardino county records only).

TYPES: Male holotype and female paratype from webs over stream on sides of 6 m diameter concrete tunnel under highway, 9–18 m inside upstream end at junction of east fork of Mountain Home Creek and Hwy 38, elev. 1586 m, San Bernardino County, California, United States (W. R. Icenogle: Aug. 24, 1990) deposited in AMNH.

ETYMOLOGY: The specific name is a noun in apposition taken from the type locality.

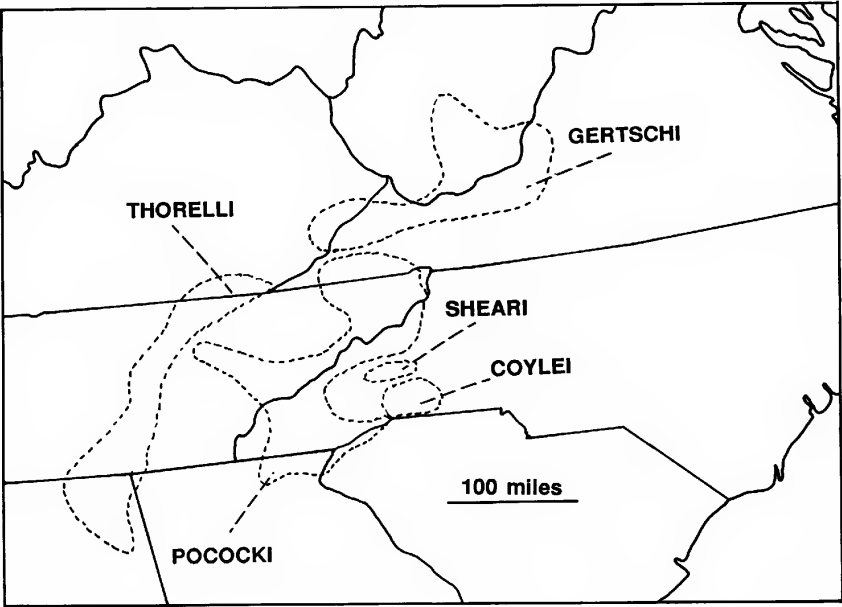
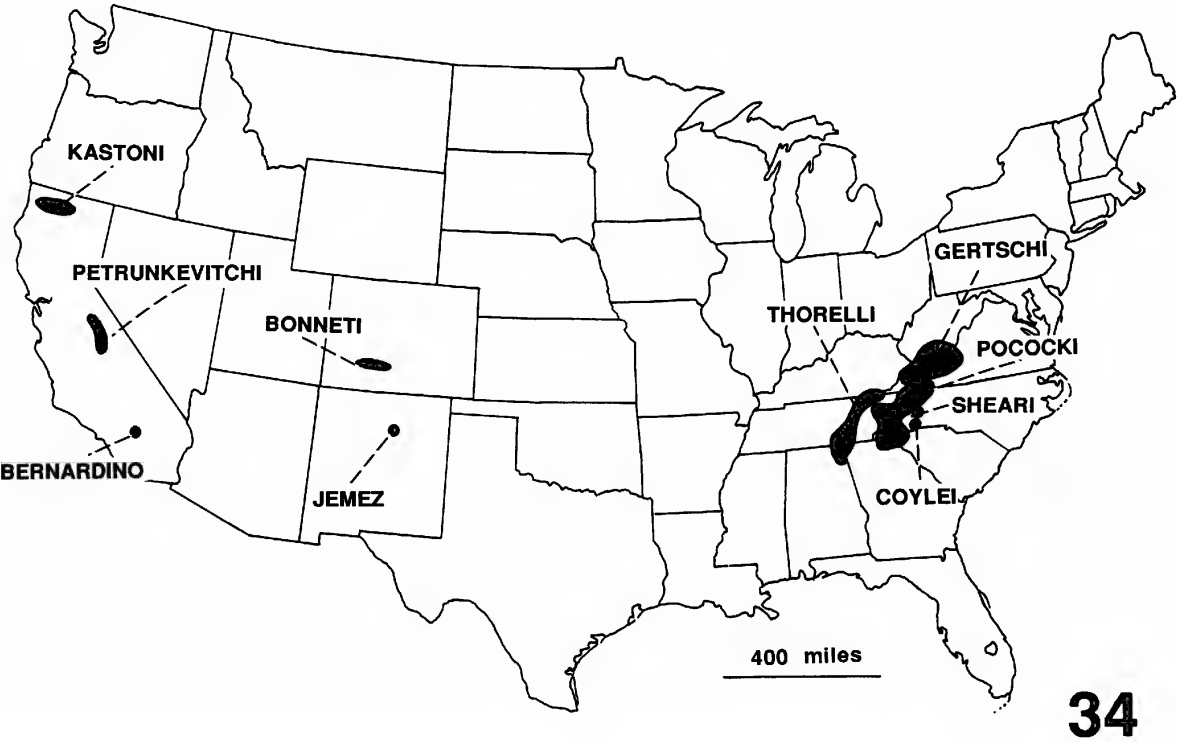
DIAGNOSIS: The species most closely resembles its sister species *Hypochilus petrunkevitchi* in general coloration, eye dimensions, and male pedipalpal morphology. Males can be recognized by the apex of the conductor which is more loosely whorled (fig. 24) than in *H. petrunkevitchi*, the shorter pedipalpal tarsus (see key), a greatly reduced distal palpal apophysis (fig. 25), and a median palpal apophysis that is significantly smaller than in *H. petrunkevitchi*, with no notch (fig. 7). The short palpal tibia is strongly incrassate proximally. Females of this species are particularly difficult to separate from *H. petrunkevitchi* females, the former possessing similar but smaller convoluted spermathecal ducts (fig. 11).

MALE: Total length 9.70. Cephalothorax 3.30 long, 2.84 wide: clypeus 0.11. Eye diameters and interdistances: AME 0.12, ALE 0.21, PME 0.21, PLE 0.21; AME–AME 0.10, AME–ALE 0.19, PME–PME 0.38, PME–PLE 0.08, ALE–PLE 0.07; MOQ length 0.38, anterior width 0.32, posterior width 0.77. Chelicerae uniformly pale yellow, no markings; promarginal cheliceral teeth 5, cheliceral formula 31452, retromarginal cheliceral teeth 2; 1 distal, 1 proximal. Endites and labium pale yellow; sternum yellow unpigmented with sparse weak setae; coxae pale yellow; trochanters with proximal and distal pigmented

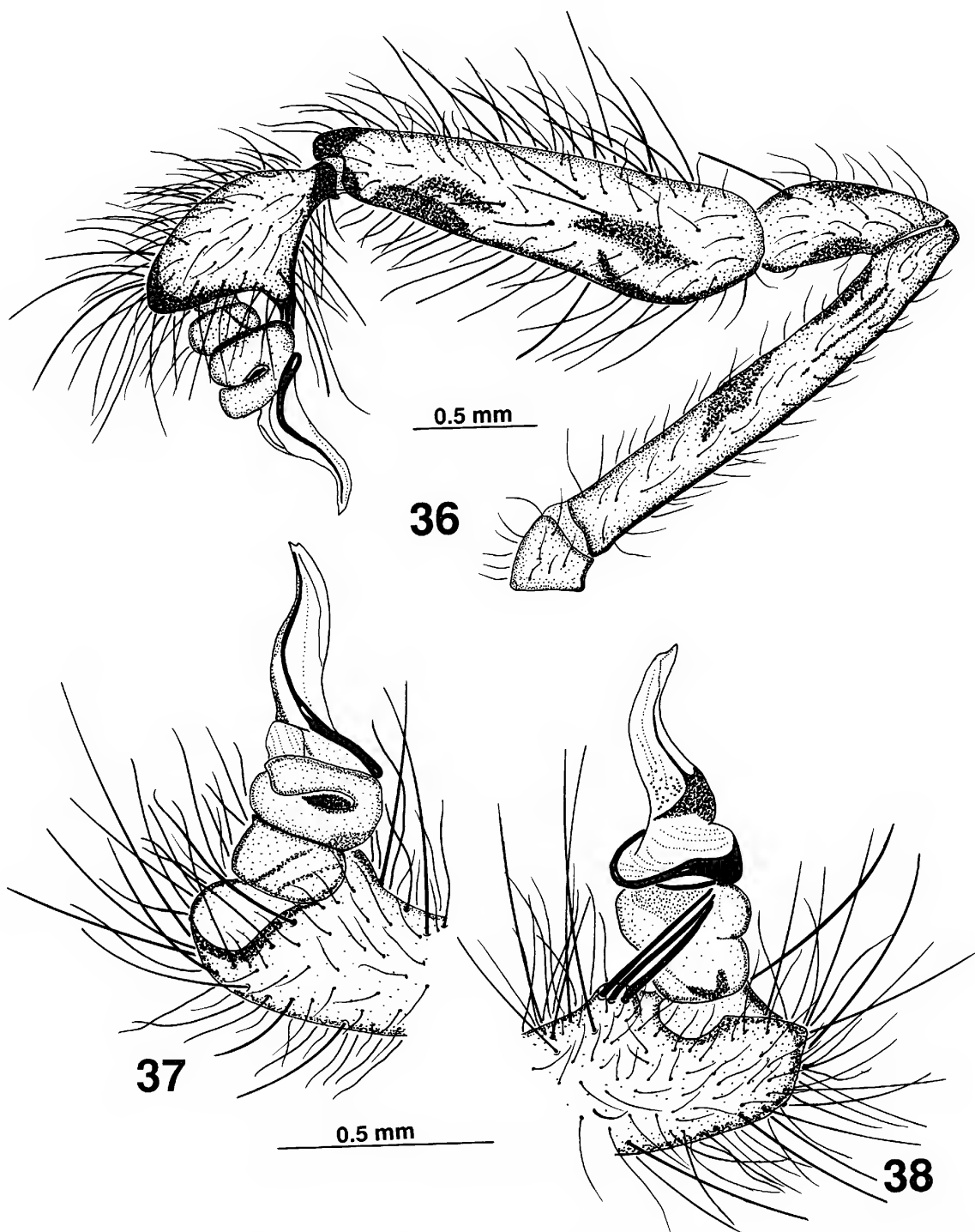
borders; all legs yellow brown with broken dark annulations on femora and tibiae; pro-lateral proximal aspect of femur 1 with approximately 15 unpigmented weak setae; leg 1 more than 19 times length of cephalothorax. Abdomen pale white with purple brown reticulations over entire surface, clothed with sparse hairs, with three transverse rows of small weak setae (fig. 39). Palpal tarsus short (0.84), palpal tibia short (1.74), very incrassate proximally (width 0.48) (figs. 36–38), PTW/PTL = 0.27, median apophysis small, PMA = 0.20 (fig. 7). Conductor of medium length (0.54) CdL/CW = 0.19; conductor tip loosely whorled with very small distal apophysis in retrolateral view (fig. 25). Leg formula 1243; spination (only surfaces bearing spines listed): Pedipalpal femur: none; tibia: d4, p9, r0; tarsus: setose with four closely appressed black spines on retrolateral surface of apical spur. Femur: I p15-0-0; II d2-0-0; III d1-0-0; IV d1-0-0. Patella: without dorsal spines. Tibia: I d1-0-0, p1-0-0, r1-0-0; II none; III d1-0-0; IV none. Metatarsus: I, v1-1-3, r0-0-1; II v1-1-1-1-3; III v0-1-5. Tarsus: I v5-4, II v5-4, III v3-2-2, IV v2-4-3. Trichobothrial distribution. All legs with: femora: none, tarsi: none, metatarsi: 1 distally, tibiae: 1 distally.

	Podite sizes				Pedi- palp
	I	II	III	IV	
Femur	21.40	1.82	11.21	11.90	2.12
Patella	1.82	1.62	1.34	1.25	0.78
Tibia	21.57	14.46	10.12	12.79	1.74
Metatarsus	15.25	11.16	8.50	10.62	—
Tarsus	4.53	4.13	3.60	4.68	0.84
Total	64.56	45.91	34.77	41.17	5.48

FEMALE: As in male except: total length 9.92, cephalothorax 4.46 long, 3.62 wide; clypeus 0.27. Eye diameters and interdistances: AME 0.11, ALE 0.27, PME 0.28, PLE 0.25; AME–AME 0.12, AME–ALE 0.25, PME–PME 0.48, PME–PLE 0.05, ALE–PLE 0.12; MOQ length 0.45, anterior width 0.36, posterior width 0.99. Clypeal area, lateral aspects of head, and foveal area darkened. Pedipalp pale yellow, darkened distally, legs pale yellow with femora and tibiae of all legs strongly annulated, first leg >9 times length of cephalothorax. Chelicerae pale yellow darkened proximally. Cheliceral teeth as in



Figs. 34, 35. 34. Distribution of *Hypochilus* species. 35. Distribution of the eastern clade of *Hypochilus* species.



Figs. 36–38. 36. Male *H. bernardino*, new species, left pedipalp, retrolateral view. 37. *H. bernardino*, palpal bulb, prolateral view. 38. *H. bernardino*, palpal bulb, retrolateral view.

male. Spermathecae with convoluted ducts and small receptacula (fig. 11). Leg formula 1243; spination (only surfaces bearing spines listed). Pedipalpal patella: d0-0-1; tibia: d1-0-0, p1-2-0; tarsus: d3-2-0, p2-1-0, v2-2-3, r1-1-1. Femur: I d5-0-0; II d2-0-0; III d1-0-0; IV d1-0-0. All tibiae without spines. Metatarsus: I d1-0-0, v3-2-3-3; II d1-1-0, v3-2-3-2; III d1-0-0, v2-3-3-2; IV v-0-0-2. Tarsus: I v2-3-0; II v2-4-2; III v4-6-1; IV v3-8-2. Trichobothrial distribution as in male except pedipalpal tibia with series of dorsal trichobothria.

	Podite sizes				Pedi- palp
	I	II	III	IV	
Femur	15.27	11.79	9.34	10.42	3.00
Patella	2.05	1.93	1.76	1.60	0.89
Tibia	14.91	11.33	8.28	9.80	2.17
Metatarsus	7.90	7.75	6.47	8.30	—
Tarsus	3.18	3.27	2.75	3.80	2.02
Total	43.31	36.07	28.60	33.92	8.10

MATERIAL EXAMINED: **California:** *San Bernardino Co.:* San Bernardino Mountains (Atkin, USNM) 1♂, 1♀; Mountain Home, matured Aug. 13, 1959 (W. J. Gertsch, V. Roth, R. X. Shick, AMNH) 1♂, 1♀; San Bernardino Mountains, junction of east fork of Mountain Home Creek and Hwy 38, Aug. 24, 1990, elev. 1586 m, in webs over stream on rock and concrete sides of 6 m diameter tunnel under highway, 9–18 m inside upstream end of tunnel (W. R. Icenogle, to be placed in AMNH) 2♂, 1♀.

DISTRIBUTION: Known only from the type locality. W. Icenogle informs me that the drought conditions in California for the last several years have had a deleterious effect on *H. bernardino* populations in southern California. In fact, the only population he was able to locate in the type locality was confined to such man-made habitats as conduit pipe. Roth (personal commun.) collected specimens from alongside Mountain Home Creek in 1959. These populations may now prove to be endangered.

Hypochilus jemez, new species
Figures 9, 31, 32, 40–43

TYPES: Male holotype and female paratype from lampshade webs on walls and roof of Terrero Cave, Terrero, 12 mi N Pecos,

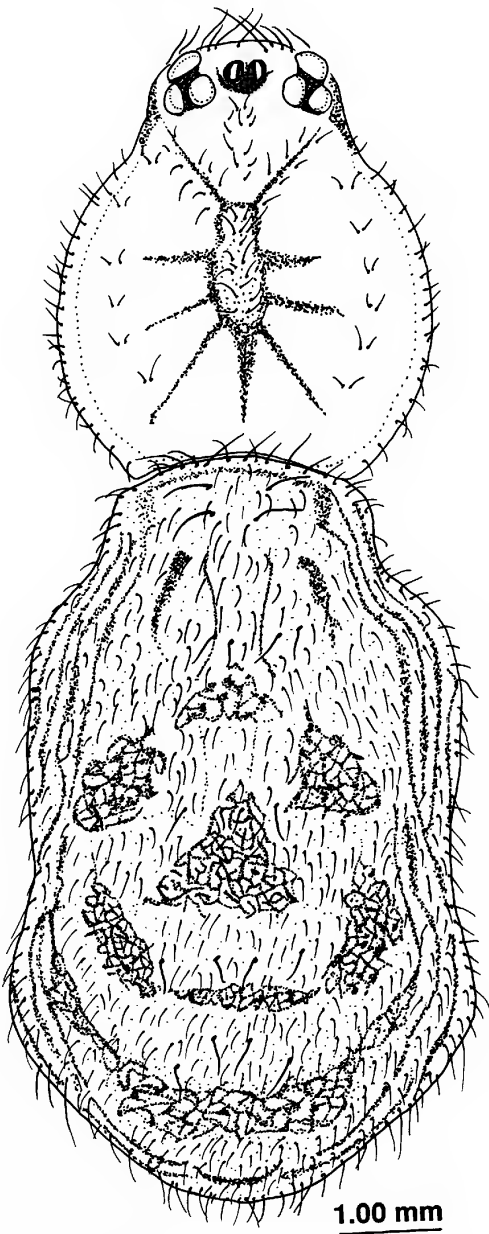
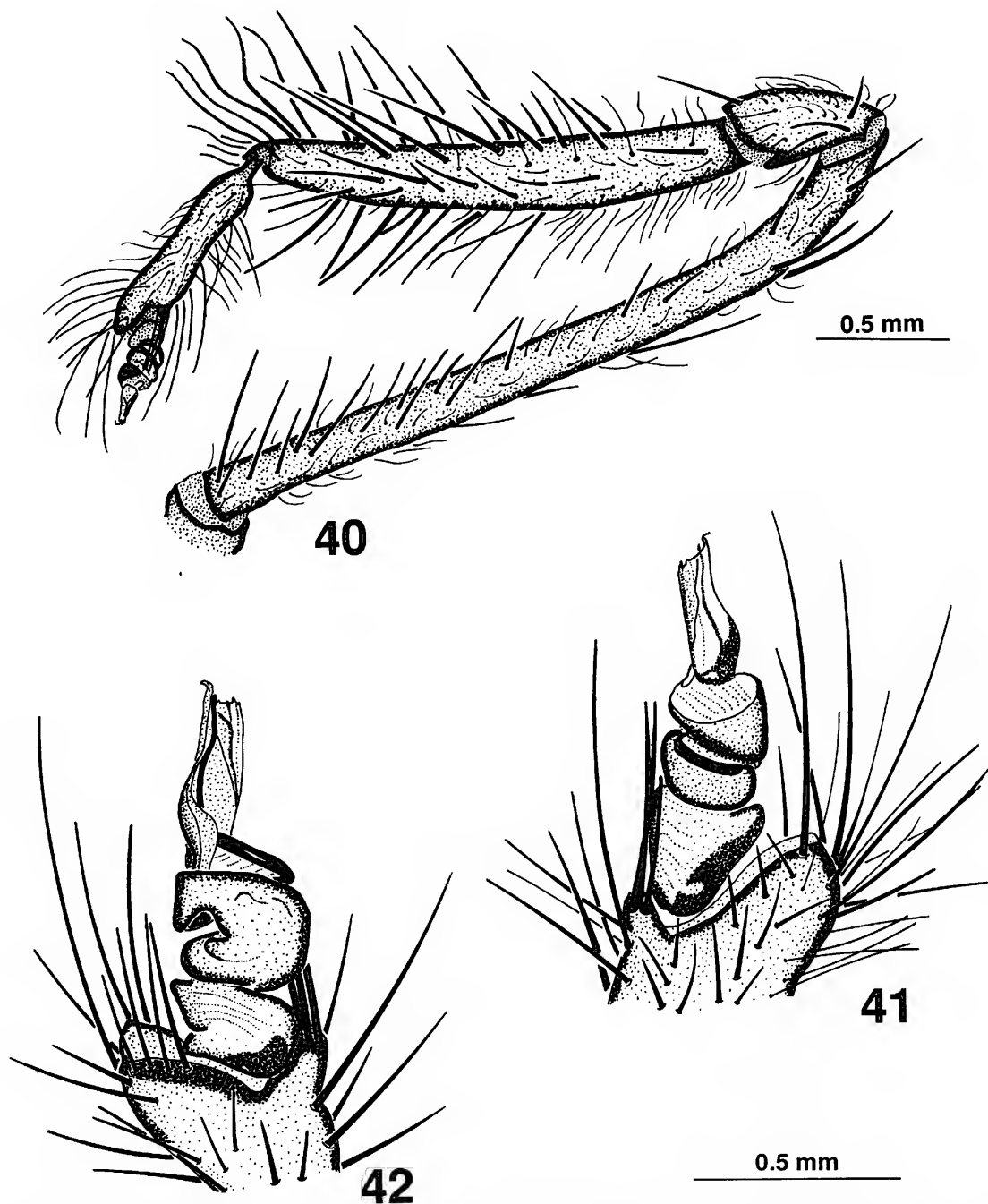


Fig. 39. *H. bernardino*, new species, cephalothorax and abdomen of male, dorsal view.

elev. 2348 m, San Miguel County, New Mexico, United States (male, K. M. Catley and D. Loch, Aug. 12, 1992; female, D. Lowrie, Nov. 21, 1990) deposited in AMNH.

ETYMOLOGY: The specific name is a noun in apposition and refers to the Jemez Indian Pueblo, for whom the type locality of Terrero Cave has profound spiritual significance.



Figs. 40–42. 40. Male *H. jemez*, new species, left pedipalpal, retrolateral view. 41. *H. jemez*, palpal bulb, retrolateral view. 42. *H. jemez*, palpal bulb, prolateral view.

DIAGNOSIS: The species most closely resembles its sister species *Hypochilus bonneti* in general coloration, eye dimensions, and male pedipalpal morphology. Males can be recognized by the shape of the tip of the palpal conductor, which forms a weak hook (figs.

31, 32) (cf. strongly hooked in *H. bonneti*). The very long palpal tibia is only weakly incrassate proximally; a group of about 15 retrolateral cheliceral denticles are grouped distally. Females have distinctive spermathecal morphology; two single ducts divide apically

into two small bulbs; such an arrangement is autapomorphic for this species (fig. 9).

MALE: Total length 9.30. Cephalothorax 3.60 long, 3.20 wide; clypeus 0.26. Eye diameters and interdistances: AME 0.13, ALE 0.21, PME 0.19, PLE 0.19; AME-AME 0.11, AME-ALE 0.22, PME-PME 0.41, PME-PLE 0.06, ALE-PLE 0.11; MOQ length 0.36, anterior width 0.32, posterior width 0.78. Chelicerae uniformly orange brown, no markings; promarginal cheliceral teeth 6, cheliceral formula 214563, retromarginal cheliceral teeth as 15 small denticles clustered distally and one small tooth medially. Endites and labium pale yellow; sternum yellow unpigmented with profuse setae; coxae pale yellow, trochanters with proximal and distal pigmented borders; legs 1 and 2 red brown, 3 and 4 yellow brown with no annulations; prolateral aspect of femur 1 with 30-40 stout black setae; leg 1 more than 13 times length of cephalothorax. Abdomen pale white, unicolorous with no markings, clothed with thin hairs, dorsum paler with three transverse rows of setae (fig. 43). Palpal tarsus long (1.42), palpal tibia very long (3.38), only slightly incrassate proximally (width 0.50) (figs. 40-42), PTW/PTL = 0.14. Conductor short (0.46), CdL/CW = 0.14, conductor tip only weakly hooked (fig. 31). Leg formula 1243; spination (only surfaces bearing spines listed): Pedipalpal femur: d4, p3, r3; tibia: d8, p13, r6; tarsus: with four closely appressed black spines on retrolateral surface of apical spur. Femur: I p41-0-0; II d10-0-0; III d7-0-0; IV d14-0-0. Patella: III and IV each with one dorsal spine. Tibia: I p1-1-1, r1-2-2; II p1-1-1, r0-2-2; III d0-1-0, p0-1-1, r0-1-1; IV d0-1-0, p0-1-2, r0-0-2. Metatarsus: I d1-0-0, p1-0-0, v2-2-4, r1-0-1; II d1-0-0, p1-0-1, v2-3-4, r0-1-1; III p1-0-0, v 2-4-6, r1-0-1; IV p1-0-0, v2-2-3. Tarsus: I v2-2-2; II v2-2-2; III v0; IV v2-2-2. Trichobothrial distribution. All legs with: tarsi: none, metatarsi: 1 distally, tibiae: 1 distally, femora: none.

	Podite sizes				Pedi- palp
	I	II	III	IV	
Femur	13.07	10.45	8.75	9.83	3.56
Patella	1.86	1.73	1.61	1.64	1.04
Tibia	14.73	10.70	8.78	10.01	3.38
Metatarsus	12.77	9.77	8.31	9.67	—
Tarsus	6.06	4.73	3.90	5.10	1.42
Total	48.49	37.38	31.35	36.25	9.40

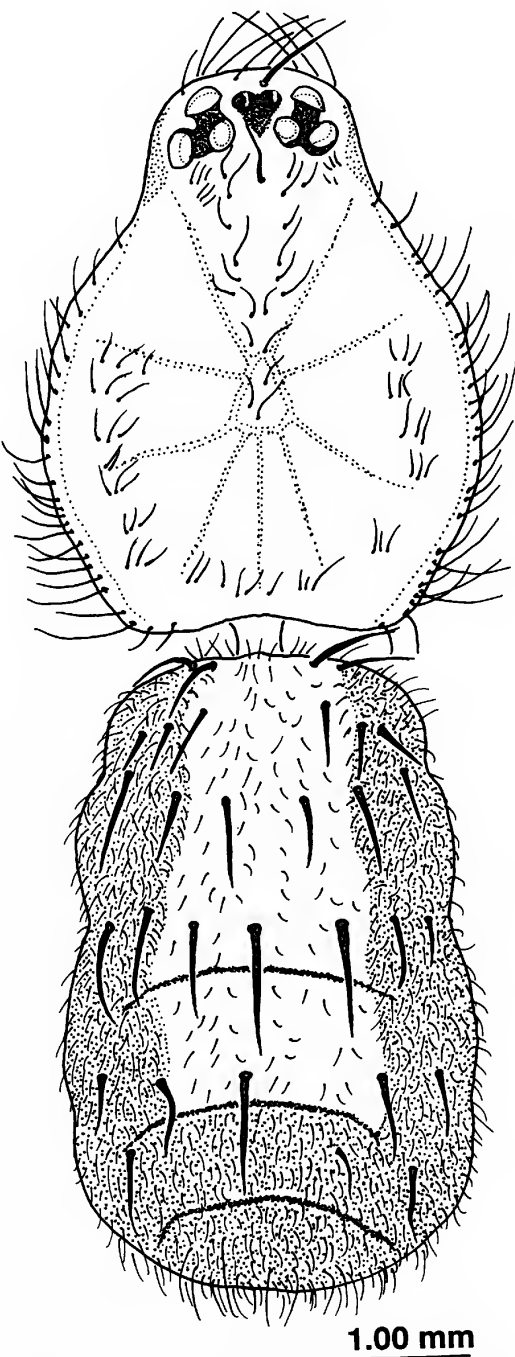


Fig. 43. *H. jemez*, new species, cephalothorax and abdomen of male, dorsal view.

FEMALE: As in male except: total length 11.50, cephalothorax 4.4 long, 3.10 wide; clypeus 0.30. Eye diameters and interdistances: AME 0.11, ALE 0.22, PME 0.21, PLE 0.24; AME-AME 0.19, AME-ALE 0.26,

PME–PME 0.45, PME–PLE 0.08, ALE–PLE 0.13; MOQ length 0.43, anterior width 0.41, posterior width 0.86. Opisthosoma with particularly strong external segmentation (fig. 43). Pedipalp pale yellow, darkened distally, legs light orange brown, no annulations, first leg only 8 times length of cephalothorax, pro-lateral and dorsal proximal aspects of femur 1 with 15 stout black setae. Cheliceral formula 231645. Spermathecae (fig. 9). Leg formula 1243; spination (only surfaces bearing spines listed): pedipalpal femur: d1-3-1, p1-0-0, r1-0-0; patella: d0-0-1; tibia: d0-2-0, tarsus: d0-1-0, p1-1-1, v2-2-3, r1-1-1. Femur: I d5-0-0, p0-7-0, r0-1-1; II d5-0-0, p0-2-1, r0-1-1; III d4-2-0, p0-1-0, r1-1-0; IV d5-2-0, p0-1-0, r1-1-0. Patella: III and IV each with one dorsal spine. Tibia: I d0-1-0, p0-2-1, r1-3-1; II d0-1-0, p0-2-1, r1-3-1; III d0-1-0, p0-1-1, r0-0-1; IV d0-1-0, p0-1-0, r1-0-0. Metatarsus: I d1-0-0, p1-0-0, v2-3-2, r0-1-1; II d1-1-0, p1-0-1, v2-3-3-2, r1-0-1; III d1-0-0, p1-0-0, v2-3-3-2, r1-1-0; IV d0-0-0, p1-0-0, v1-1-2-2, r0-0-0. Tarsus: I v2-3-2; II v2-3-2; III v2-3-2; IV v2-2-2. Trichobothrial distribution as in male except pedipalpal tibia with 1 distal, 1 medial.

	Podite sizes				Pedi-palp
	I	II	III	IV	
Femur	11.00	9.16	7.80	8.81	3.56
Patella	1.95	1.77	1.70	1.47	1.02
Tibia	10.65	9.21	7.52	8.55	2.94
Metatarsus	9.04	8.06	6.62	8.44	—
Tarsus	4.32	3.63	3.20	3.91	2.30
Total	36.96	31.83	26.84	31.18	9.82

MATERIAL EXAMINED: **New Mexico:** *San Miguel Co.:* Terrero Cave, Terrero, 12 mi N Pecos, elev. 2350 m, rock ledges and walls of cave (D. Lowrie, Nov. 21, 1990) 1♂, 1♀, 3 imm.; same locality, Aug. 12, 1992 (K. M. Catley, D. Loch) 3♂, 5♀, 9 imm. Dalton Canyon Creek (5 mi N of Lisboa Springs Fish Hatchery on Rt. 63) limestone outcrop on the west bank of creek 1 mi up canyon, elev. 2250 m, Aug. 18, 1992 (K. M. Catley, D. Loch) 1♂. All material deposited in the AMNH.

DISTRIBUTION: Known only from the type locality, Terrero Cave, and the immediate surrounding area of the Pecos River watershed, New Mexico.

DISTRIBUTION AND NATURAL HISTORY

During June 1975 and February 1976 *Hypochilus* immatures were collected from Terrero Cave by W. C. Welbourn. They were determined by W. J. Gertsch to be *H. bonneti* and deposited in the AMNH. In 1990 Dr. D. Lowrie collected a single male and female from the cave; I determined that they represented a new species. Subsequently I visited the site to increase the sample size and determine the distribution.

Terrero Cave in the Pecos Canyon is located at the southern edge of the Sangre de Cristo range, which represents a southern extension of the Rocky Mountains. The heavily wooded area is an upland corridor of montane conifer forest bounded on the east by low dry grasslands and to the west by the broad river valley of the Rio Grande. Beyond to the south lies dry desert scrub, an area patently unsuitable as *Hypochilus* habitat. Climatic data are available for Pecos which lies some 12 m to the south and is 250 m lower than the cave. The mean daily maximum and minimum temperatures in 1991 were 25.8°C and 10.1°C for July and 5.2°C and –11.3°C for January, with annual mean ranges typically 32°C to –28°C. Precipitation falls mainly during the late summer and early fall with a 20-year average (1970–1989) of 41 cm annually (Jenks, New Mexico Department of Fish and Game, personal commun.). The higher elevation of Terrero Cave results in cooler temperatures and increased precipitation.

The canyon exhibits vegetational zonation from drier pinyon and juniper scrub at the lower end, through pine and scrub oak to spruce and aspen at the upper reaches. The largest population of *H. jemez* was found inside Terrero Cave; however, the animal is able to survive in marginal habitat outside the cave. Observation of seven occupied web sites outside the cave for four consecutive days showed that, unlike the eastern clade and the cave population, populations of *H. jemez* outside the cave frequent their webs only at night.

Outside the cave, webs were found on weathered granite or limestone. Microhabitat requirements appear to include a sufficiently

dense canopy cover to provide partial shade. However, dense cover promotes bryophyte growth on the rock surface which, as in the eastern species, is avoided for web building. Deep fissures in the rock close to the web site that allow the spider access to a dark diurnal retreat are also necessary. Areas of pinyon and juniper toward the lower reaches of the valley are apparently too open and dry for *Hypochilus*.

Despite a diligent search of the canyon from the Lisboa Springs Fish Hatchery to Cowles and beyond (a distance of 25 mi), we were only able to find *Hypochilus* at the following locations. (1) Seven webs and four web scars on granite outcrops on the west bank of the Pecos above Windy Bridge picnic site, elev. 2300 m. (2) Two webs and one web scar on roadside granite outcrops, east bank of the Pecos River 0.7 mi N of Windy Bridge, elev. 2350 m. (3) One web with juvenile and numerous old (at least one year old and probably more) eggs sacs in a disused stone pump-house on the east bank of Holy Ghost Creek 0.1 mi N of the entrance to Terrero campsite, elev. 2350 m. (4) One web (containing a very small but mature male) in limestone outcrop on the west bank of creek 1 mi up Dalton Canyon Creek (5 mi N of Lisboa Springs Fish Hatchery on Rt. 63), elev. 2250 m. (5) Two webs and spiderlings from limestone outcrop alongside trail 2 mi N of Cowles trail head on Cave Creek, elev. 2750 m. The Cave Creek caves (the only other limestone caves in the area, 3 mi NW Cowles) were carefully searched but no sign of webs could be found, apart from one (very old?) web scar on limestone some 20 m upstream of the cave entrance. Recent scouring of the walls and roof of the caves by floodwater make them unsuitable habitat for *Hypochilus*.

The population in Terrero Cave, on the other hand, seems healthy, with an age structure comprising all life stages—adult males, adult females, juvenile animals, recently eclosed spiderlings and newly constructed, as well as old, egg sacs. Such population structure suggests that, within the stable environment of the cave, breeding may occur throughout the year and be limited only by food supply, which within the cave appears to be based on two dipteran species, *Drosophila rubrifrons* Patterson and Wheeler and

a mycetophilid, *Orfelio* sp., both of which occur in the cave in vast numbers. Only two spiders were observed feeding, both on mycetophilids. Despite the fact that isopods were fairly common, none were found in webs. Spiders from the eastern clade vibrate rapidly in their webs when disturbed, followed normally by dropping from the web (personal obs.). This behavior was not observed in *H. jemez* either in populations from the cave or outside. When disturbed these spiders simply walk rapidly out of the web.

Webs of primarily juvenile animals were found on the walls and ceiling of the main cavern from within 8 m of the entrance to the back wall (approximately 40 m) where a small amount of light penetrated. Web structure is similar to that in the eastern clade but the lampshade is shallower and less frameline structure is apparent. Breeding populations were confined to drier areas in the first fissure off to the left of the main cavern; these, however, are narrow and very difficult to reach and in areas of total darkness. A second passage off to the left continues for some 25 m; many of the early sections were wet and appeared to be scoured by floodwater, so no webs were found. At the end of this passage the rock is fairly dry, while the roof lowers to less than a meter. Here, among depressions in the roof, another strong population comprising mature females, juveniles, and egg sacs (some concealed behind veil webs; Catley, 1993) was found. The passageway leading off to the right from the back of the main cavern was searched for a considerable distance (approximately 350 m). Due to frequent scouring by floodwater many of the walls and ceilings of this cavern were covered in thick mud and were not suitable for web building. A careful search of Terrero Cave resulted in the following population estimate: mature males 3, mature females 17, juveniles 48.

A careful search of apparently suitable habitat for some 100 mi north of the Pecos watershed at the following locations did not reveal any *Hypochilus* populations. (1) Taos Co.: Tres Ritos, La Junta Canyon, elev. 2850 m. (2) Taos Co.: 5 mi N Tres Ritos area between Comales and Ostia Canyons on Rt. 518, limestone outcrops, elev. 2450 m. (3) Taos Co.: watersheds between Rio Pueblo and Taos on Rt. 518. (4) Taos Co.: red granite

outcrops along Red River Valley on Rt. 38. (5) Colfax Co.: Cimarron Canyon, Rt 38, 4 mi E Eagles Nest, elev. 2350 m. It may be significant that the dictynid *Mallos trivittatus* Banks, which also builds its extensive web on rock faces, is very common throughout the area.

The significance of the Hypochilidae lies in its "phylogenetic uniqueness" (Nixon and Wheeler, 1992) as the sister group to all other araneomorph spiders (Forster et al., 1987). In order to maximize biodiversity, where the protection status of two species may be in conflict, small clades that represent the sister group to much larger clades should be given preference over any individual species of the larger clade if we are to make any real strides in conservation (Platnick, 1991). Given that Terrero Cave and the immediate Pecos watershed is a refugium for *H. jemez* and that this species is basal in the genus it should be evaluated for immediate conservation priority.

CLADISTIC ANALYSIS

Thirteen of the surveyed characters exhibited sufficient interspecific variation to be useful in the cladistic analysis. Character states and their hypothesized polarity were defined as follows (unless stated otherwise, the first state is hypothesized as plesiomorphic).

0. PTaM (black "thumbprint mark" on retrolateral surface of male pedipalpal tarsus); absent or present (fig. 3).

1. SP (intensity of dark pigmentation on male sternum); absent, light, heavy.

2. CdL (length in mm of male palpal conductor in retrolateral view); short (0.45–0.60) vs. long (0.70–1.00) (fig. 2).

3. PTaL (length in mm of male pedipalpal tarsus in retrolateral view); long (>2.5) vs. short (<1.3) (fig. 3).

4. AME (diameter of anterior eye pupil in mm); small (0.07–0.12) vs. large (0.16–0.24).

5. PTW/PTL (shape of male pedipalpal tibia, maximum width in retrolateral view/length in retrolateral view in mm); long and narrow (0.11–0.15), medium (0.17–0.22), short and wide (0.24–0.29) (fig. 1).

6. Spermathecal ducts; not convoluted vs. convoluted (figs. 9–18).

7. Primary web construct; sheet vs. lampshade.

8. Sigilla; three pairs clearly defined vs. poorly defined labial sigilla only.

9. APC (shape of apex of conductor); boat-shaped, hooked, twisted, corkscrewed, beak-shaped (figs. 21–31).

10. PCT (number of promarginal cheliceral teeth); 8, 6, or 5 (fig. 19).

11. CTre (retromarginal cheliceral teeth); 1–6 large teeth distributed along entire length vs. group (6–15 denticles) situated distally (fig. 19).

12. Palpal conductor distal apophysis; absent or present (figs. 24, 25).

Table 1 shows quantitative character values for males of each of the 10 *Hypochilus* species and for *E. davidi* (the outgroup).

The cladogram (fig. 44) expresses my hypothesis of the species relationships of the genus *Hypochilus* and supports the following phylogeny: (Rocky Mountain clade + (Sierra Nevada clade + Appalachian clade)). Exact analysis produced by the ie function of Hennig86 resulted in two equally parsimonious cladograms requiring 22 steps, CI 0.86, RI 0.91. The preferred topology (fig. 44) was achieved by alternative optimization (reversals) of characters 5 (the shape of male pedipalpal tibia) and 6 (convoluted spermathecal ducts). As I consider these characters homologous in *H. petrunkevitchi*, *H. bernardino*, and *H. gertschi*, the preferred topology is congruent with that hypothesis. The alternative topology (fig. 45) differs in the optimization of characters 5 and 6 (as parallelisms) and is also less resolved vis-à-vis *H. kastoni* and *H. pococki*. A more resolved tree, as well as being more informative, is also easier to falsify, a further reason to prefer the first topology.

KEY TO SPECIES

Ranges given for males are based on sample sizes shown in table 1. Due to the especially small sample sizes of females, most characters in the key to females should be used with caution. However, the clearly defined allopatric ranges of each species provide an excellent diagnostic character.

1. Males	2
Females	11

TABLE 1
Quantitative Character Values for Males of *Hypochilus* and *Ectatosticta davidi*. Abbreviations defined in methods section; range, mean, and standard deviation given for each character (all measurements in mm)

Species	N	PTW/PTL	CdL	AME	AMEi	PTaL	PMA	CTre	PCT
<i>gertschi</i>	6	0.265-0.286 0.276 ± 0.008	0.714-0.824 0.714 ± 0.04	0.165-0.201 0.18 ± 0.014	0.165-0.201 0.174 ± 0.015	0.93-0.99 0.967 ± 0.023	0.016-0.038 0.029 ± 0.009	1	5
<i>thorelli</i>	5	0.167-0.211 0.190 ± 0.016	0.695-0.897 0.792 ± 0.073	0.128-0.183 0.159 ± 0.022	0.183-0.201 0.192 ± 0.06	0.95-1.15 1.065 ± 0.096	0.027-0.043 0.032 ± 0.006	3-4	5
<i>pococki</i>	6	0.187-0.237 0.211 ± 0.017	0.824-0.952 0.869 ± 0.047	0.183-0.22 0.207 ± 0.015	0.192-0.275 0.227 ± 0.028	1.06-1.15 1.089 ± 0.032	0.023-0.032 0.029 ± 0.004	2-5	5
<i>coylei</i>	4	0.159-0.184 0.176 ± 0.011	0.897-1.007 0.938 ± 0.053	0.192-0.21 0.199 ± 0.008	0.22-0.238 0.226 ± 0.08	1.17-1.23 1.244 ± 0.054	0.038-0.045 0.042 ± 0.003	4-6	6
<i>sheari</i>	4	0.197-0.209 0.201 ± 0.006	0.787-0.824 0.803 ± 0.019	0.201-0.238 0.22 ± 0.15	0.183-0.22 0.201 ± 0.021	1.02-1.09 1.057 ± 0.031	0.033-0.042 0.038 ± 0.004	2	6
<i>kastoni</i>	3	0.189-0.213 0.203 ± 0.013	0.54-0.575 0.561 ± 0.018	0.101-0.11 0.105 ± 0.004	0.11-0.128 0.117 ± 0.01	0.80-0.86 0.838 ± 0.029	0.015-0.020 0.017 ± 0.002	2	5
<i>bonneti</i>	4	0.143-0.156 0.150 ± 0.006	0.45-0.512 0.487 ± 0.03	0.073-0.112 0.093 ± 0.19	0.10-0.128 0.116 ± 0.012	1.10-1.21 1.154 ± 0.045	0.015-0.023 0.018 ± 0.004	6-7	5
<i>bernardino</i>	4	0.245-0.266 0.257 ± 0.009	0.549-0.586 0.567 ± 0.015	0.101-0.146 0.119 ± 0.02	0.064-0.092 0.078 ± 0.012	0.80-0.91 0.847 ± 0.046	0.012-0.021 0.018 ± 0.004	2	5
<i>petrunk.</i>	4	0.251-0.286 0.264 ± 0.016	0.586-0.668 0.634 ± 0.38	0.092-0.146 0.115 ± 0.023	0.064-0.128 0.101 ± 0.029	0.95-1.1 1.013 ± 0.078	0.024-0.033 0.028 ± 0.004	2	5
<i>jemez</i>	4	0.135-0.141 0.139 ± 0.002	0.46-0.531 0.498 ± 0.3	0.078-0.13 0.101 ± 0.022	0.109-0.119 0.114 ± 0.047	1.29-1.42 1.35 ± 0.067		14-15	6
<i>E. davidi</i>	1	0.150	0.493	0.138	0.175	2.60	0.018 0.013	9	8

TABLE 2
Data Matrix

<i>Ectatosticta</i>	00000	00000	000
<i>gertschi</i>	11111	21113	100
<i>thorelli</i>	12111	10114	100
<i>pococki</i>	11111	10113	100
<i>coylei</i>	12111	10114	200
<i>sheari</i>	12111	10114	200
<i>kastoni</i>	01010	10112	100
<i>bonneti</i>	00010	00111	110
<i>bernardino</i>	01010	21112	101
<i>petrunkevitchi</i>	01010	21112	101
<i>jemez</i>	00010	00111	210

2. PTaM (fig. 3) present; CdL long (0.7–1.00 mm) (fig. 2); AME large (0.12–0.24 mm); AMEi wide (0.16–0.27 mm); eastern United States 3
PTaM absent; CdL short (0.54–0.68 mm); AME small (0.07–0.12 mm); AMEi narrow (0.06–0.13 mm); western United States 7

3. SP heavy 4
SP light or absent 6

4. F1M present (fig. 20) 5
F1M absent; CTre = 3–4; palpal tibia short with no noticeable proximal swelling (PTW/PTL = 0.17–0.21); APC beak-shaped but with truncated blunt apex (fig. 28); Cumberland Plateau from extreme western Virginia and southeastern Kentucky, south into extreme northwestern Georgia and northern Alabama (fig. 35) *H. thorelli*

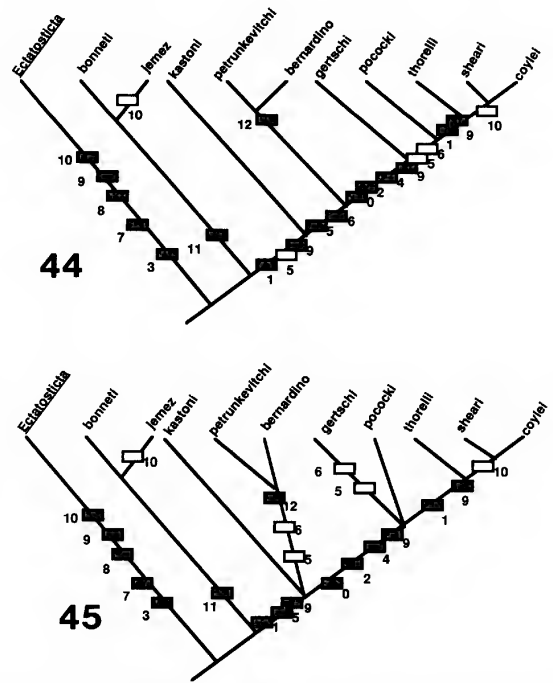
5. CTre = 2; palpal tibia short with swollen proximal region (PTW/PTL = 0.20–0.21); APC strongly beak-shaped with upwardly directed end (fig. 30); Buncombe and McDowell counties of western North Carolina (fig. 35) *H. sheari*
CTre = 4–6; palpal tibia short with no proximal swelling (PTW/PTL = 0.16–0.18); APC with less pronounced beak-shape and downwardly directed end (fig. 29); Henderson, Polk, and Rutherford counties of western North Carolina (fig. 35) *H. coylei*

6. CTre = 1 (rarely 4); palpal tibia short with greatly enlarged proximal region (fig. 6) (PTW/PTL = 0.26–0.28); APC with slight cork-screwing, apex blunt and solid (fig. 26); southern West Virginia, bordering areas of Kentucky and Virginia (fig. 35) *H. gertschi*
CTre highly variable, 2–5; palpal tibia with somewhat enlarged proximal region (PTW/PTL = 0.18–0.23); APC strongly cork-screwed with apex open (fig. 27); Blue Ridge Mountains of western Virginia and eastern Tennessee, through western North Carolina and into northwestern South Carolina (fig. 35) *H. pococki*

7. F1M present (fig. 20) 8
F1M absent 9

8. CTre = 6–9 small denticles clustered distally, no proximal teeth; PTaL long (1.10–1.21); palpal tibia long and narrow with only slight proximal swelling (PTW/PTL = 0.14–0.15) (fig. 2); APC with prominent, strongly twisted hook (fig. 20); central Colorado (fig. 34) *H. bonneti*
CTre = 14–15 small denticles clustered distally with one large medial tooth; PTaL very long (1.29–1.42); palpal tibia relatively longer with insignificant proximal swelling (PTW/PTL = 0.13–0.14) (figs. 31, 32); APC weakly hooked (figs. 40–42); known only from San Miguel county, New Mexico (fig. 35) *H. jemez*

9. Palpal tibia not enlarged proximally (PTW/PTL = 0.19–0.21); PTaL short (0.81–0.86



Figs. 44, 45. 44. Cladogram of hypothesized relationships of *Hypochilus* species. Preferred topology of two most parsimonious trees produced by the implicit enumeration function of Hennig86, length 22, CI = 86, RI = 91. 45. Topology of other most parsimonious tree with characters 5 and 6 optimized as parallelisms. Black character boxes represent forward changes, white boxes homoplasious characters; see text for explanation.

Tennessee, through western North Carolina and into northwestern South Carolina (fig. 35) *H. pococki*

7. F1M present (fig. 20) 8
F1M absent 9

8. CTre = 6–9 small denticles clustered distally, no proximal teeth; PTaL long (1.10–1.21); palpal tibia long and narrow with only slight proximal swelling (PTW/PTL = 0.14–0.15) (fig. 2); APC with prominent, strongly twisted hook (fig. 20); central Colorado (fig. 34) *H. bonneti*
CTre = 14–15 small denticles clustered distally with one large medial tooth; PTaL very long (1.29–1.42); palpal tibia relatively longer with insignificant proximal swelling (PTW/PTL = 0.13–0.14) (figs. 31, 32); APC weakly hooked (figs. 40–42); known only from San Miguel county, New Mexico (fig. 35) *H. jemez*

9. Palpal tibia not enlarged proximally (PTW/PTL = 0.19–0.21); PTaL short (0.81–0.86

- mm); APC a tight coil with inwardly directed end (figs. 22, 23); Humbolt and Siskiyou counties of northern California (fig. 35) *H. kastoni*
 Palpal tibia enlarged proximally (PTW/PTL = 0.24–0.28); central or southern California 10
10. PTaL long (0.99–1.10 mm); PMA large (0.02–0.03) and strongly notched at proximal edge (fig. 8); APC in tight whorl with large inwardly directed distal apophysis (fig. 24); Fresno, Mariposa, and Tulare counties of central California (fig. 35) *H. petrunkevitchi*
 PTaL shorter (0.80–0.91 mm); PMA small (0.01–0.02) with no notch (fig. 7); APC more loosely whorled with very small inwardly directed distal apophysis (fig. 25); San Bernardino county in southern California (fig. 35) *H. bernardino*
11. Spermathecal ducts convoluted (figs. 11–13) 12
 Spermathecal ducts not convoluted (figs. 9, 10, 14–18) 14
12. Spermathecal median ducts $\leq$ length of lateral ducts; spermathecae as in figure 12; southern West Virginia, bordering areas of Kentucky and Virginia *H. gertschi*
 Spermathecal median ducts $\geq$ length of lateral ducts; California 13
13. Spermathecal bulbs large, diameter of largest not less than 0.11 mm; median ducts of greater length than lateral ducts; spermathecae as in figure 13; Fresno, Mariposa, and Tulare counties of central California *H. petrunkevitchi*
 Spermathecal bulbs small, diameter of largest does not exceed 0.083 mm; median ducts $\geq$ length of lateral ducts; spermathecae as in figure 11; San Bernardino county in southern California *H. bernardino*
14. Spermathecal bulbs on each side enter into a single duct (fig. 9); bulbs very small, diameter of largest bulb does not exceed 0.073 mm; known only from San Miguel county, New Mexico. *H. jemez*
 Each spermathecal bulb with its own duct 15
15. Spermathecal bulbs small (diameter < 0.11 mm); western United States 16
 Spermathecal bulbs large (diameter > 0.11 mm); eastern United States 17
16. Ducts narrow, bulbs small, diameter of largest does not exceed 0.064 mm; central Colorado; spermathecae as in figure 16 *H. bonneti*
 Ducts broad, bulbs large, diameter of largest not less than 0.109 mm; spermathecae as in figure 10; northern California *H. kastoni*
17. Lateral ducts short, originating on median ducts; bulbs moderately globose, diameter of largest not less than 0.185 mm; spermathecae as in figure 17; Buncombe and McDowell counties of western North Carolina *H. sheari*
 Lateral ducts long, not originating on median ducts 18
18. Median bulbs not globose, diameter of largest does not exceed 0.12 mm; spermathecae as in figure 18; Henderson, Polk, and Ruth-erford counties of western North Carolina *H. coylei*
 Median bulbs very globose, diameter of largest not less than 0.24 mm 19
19. Lateral ducts short and tubular with diameter of largest bulb not less than 0.24 mm; spermathecae as in figure 15; Blue Ridge Mountains of western Virginia and eastern Tennessee, through western North Carolina and into northwestern South Carolina *H. pococki*
 Lateral ducts extremely short, almost contiguous with bursa copulatrix; bulbs not globose, diameter of largest does not exceed 0.14 mm; spermathecae as in figure 14; Cumberland Plateau from extreme western Virginia and southeastern Kentucky, south into extreme northwestern Georgia and northern Alabama *H. thorelli*

DISCUSSION

The paucity of the early spider fossil record (Shear and Kukalova-Peck, 1990) and complete lack of fossil evidence regarding the hypochiloid and austrochiloid spiders (Hypochilidae: Austrochilidae, and Gradungulidae) allow only for conjecture concerning their early history. Whereas Mesothelae-like spiders are known as early as the Middle Devonian (Selden et al., 1991), araneomorph spider fossils are not known earlier than the Lower-Middle Jurassic. The earliest documented araneomorph aerial web-spinning spiders can clearly be placed in modern families or superfamilies. Eskov (1984, 1987) described an extinct orbweaver family, the Juraraneidae, as well as an archaeid from the Jurassic, while Selden (1989, 1990) described fossils from the Lower Cretaceous which he placed in the Deinopoidea and Araneoidea. The early radiation in the Araneoidea was evidently preceded by an even earlier ap-

pearance of hypochilid progenitors, perhaps during the Carboniferous. The modern distribution of hypochiloids and austrochiloids in Asia, North America, Australasia, and temperate South America, suggests that early araneomorphs were widely distributed prior to the breakup of Pangaea. Cribellate silk and lighter body weight would have allowed radiation into habitats previously unavailable to the Mygalomorphae or Mesothelae.

The contemporary montane distribution of hypochilids appears strongly influenced by moisture gradients. The most speciose (and also the most apomorphic) clade comprising *H. gertschi*, *H. pococki*, *H. thorelli*, *H. coylei*, and *H. sheari* is known only from the southern Appalachian Mountains (fig. 35), where it occupies an altitudinal range of approximately 305–1525 m. Preferred habitats are overhanging rock ledges normally close to running water (Fergusson, 1972; personal obs.); in addition these spiders are infrequently found on tree trunks (personal obs.), the entrance zone of caves (Forster et al., 1987; personal obs.), as well as deep in the dark zone of caves (this paper). The far western clade, comprising *H. petrunkevitchi*, *H. bernardino*, and *H. kastoni*, occurs in, respectively, the Sierra Nevada in central California (549–2135 m), the San Bernardino Mountains of southern California (1586 m), and the Cascade Range in northern California (1372 m) (fig. 34). Recorded habitats for these species include granite overhangs and bases of waterfalls (*H. petrunkevitchi*) (Forster et al., 1987) and the ceilings of water-carrying steel conduit pipe (*H. bernardino* and *H. kastoni*) (W. Icenogle, personal commun.).

Although *H. bonneti* is apparently confined to caves and deep canyons of the Colorado Plateau in central Colorado (1769–2135 m) (fig. 34), it is probably widely distributed in such habitats (Gertsch, 1964). *H. jemez* is found only at the southern edge of the Sangre de Cristo mountains, New Mexico (2348 m) (fig. 34); together with its sister species *H. bonneti*, they form the most plesiomorphic clade. All species of *Hypochilus*, especially the western clades, are under-collected. Although the restricted range of *H. jemez* has been carefully determined (this paper), it is to be expected that the known range of *H.*

kastoni in particular will be extended by further collecting in suitable habitat.

There are two especially prominent disruptive events which might have split *Hypochilus* into western and eastern clades: either the Lower Cretaceous marine inundations of North America which formed a barrier from the Gulf of Mexico to Canada, or the much later demise of the broad band of Arcto-Tertiary vegetation across central North America. It is unlikely that the older event created the disjunction evident in the cladogram because there is no evidence of secondary east-west speciations which one would reasonably expect to have resulted from the later Arcto-Tertiary forest retreat. For this and other reasons discussed below, the second scenario seems more plausible.

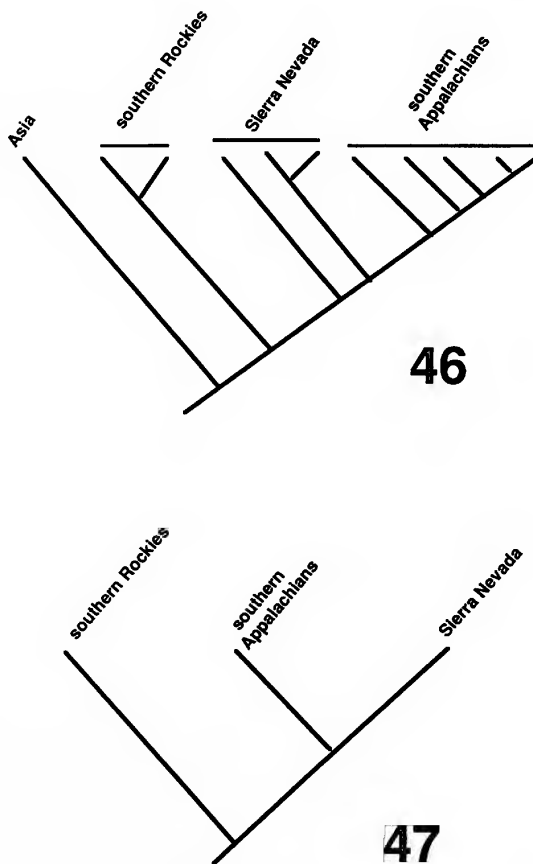
The east-west disjunction seen in *Hypochilus* (fig. 34) is mirrored in several other hygrophilous taxa including the mygalomorph spiders *Antrodiaetus* and *Atypoides* (Coyle, 1971), the millipede family Xystodesmidae (Hoffman, 1963b), and perhaps most strikingly in the plethodontid salamander genus *Aneides* (Lowe, 1950; Wake, 1963, 1966; Macgregor and Jones, 1977). From skeletal synapomorphies presented by Lowe (1950), *Aneides* does appear to be monophyletic and therefore inferences drawn from its distribution are valid. The disjunction seen in *Aneides* into an *aeneus* species group in the southern Appalachians, a *lugubris* species group in the Far West, and *A. hardii* at the southern end of the Rocky Mountains in New Mexico, is closely paralleled by *Hypochilus*. Equally interesting is the conclusion, based on comparative osteology (Wake, 1963), that in this genus, as in *Hypochilus*, the Rocky Mountain species are the most plesiomorphic. Two important characteristics which both these taxa share, and which may help explain their common geographical patterns, are low vagility and a high susceptibility to desiccation, which enforce strong coupling to a moist forest environment. Such correlations (habitat requirements and observed distribution patterns) provide circumstantial evidence to support the hypothesis of a late Tertiary date for the major east-west disjunction of *Hypochilus*. Reduced taxon-area cladograms for *Hypochilus* and *Aneides* (figs. 46, 47) are largely congruent and support the

hypothesis that the Southern Rockies are the sister area of the Sierra Nevada plus the Appalachians.

Extensive deciduous forests across central North America up to the late Tertiary (Miocene-Pliocene) (Axelrod, 1960) probably provided the last link between eastern and western populations of *Hypochilus*. A combination of a cooler, drier climatic regime established during the Oligocene, together with the rain shadow imposed by the newly uplifted Rockies, replaced the transcontinental Arcto-Tertiary forest with savannah-type vegetation by the close of the Tertiary (Wake, 1966; Mizuno and Macgregor, 1974; Thomas and Spicer, 1987). Assuming these spiders were constrained by moisture requirements like those of their modern counterparts, they would have been unable to maintain contiguous populations across central North America.

Hoffman (1963a) first pointed out the similarities between *H. gertschi* in the east and *H. petrunkevitchi* in California, and proposed that the common ancestor of these species was a transcontinental taxon which was split into western and eastern clades. My cladogram is congruent with this hypothesis on the strength of two synapomorphies (shared by *H. gertschi*, *H. petrunkevitchi*, and its sister species *H. bernardino*), the shape of the palpal tibia (PTW/PTL: fig. 1), and convoluted spermathecal ducts (figs. 11–13). Convoluted spermathecal ducts have been lost in subsequent sister taxa, although the general evolutionary trend of shorter, wider palpal tibiae (cf. longer, thinner in the Rocky Mountain clade), is seen in both *H. kastoni* and all of the eastern clade. Of possible importance too is *H. gertschi*'s apparent increased tolerance of drier conditions (Hoffman, 1963a; Coyle, personal commun.), which may have allowed *H. gertschi* or its ancestor the wider environmental tolerance required for a transcontinental distribution prior to the postulated east-west disjunction in the Tertiary.

I have observed (both in the field and laboratory) that *H. pococki* (Catley, 1993) and *H. jemez* (this paper) females sometimes screen off newly constructed egg sacs in a rock crevice by means of a vertical sheet web. Such webs contain no cribellate silk and therefore differ greatly in form and texture from regular



Figs. 46, 47. Taxon-area cladograms. 46. *Hypochilus*. 47. Plethodontid salamander genus *Aneides*, based on Lowe (1950).

lampshade webs. More significantly, such sheet webs are often constructed by young (second instar?) spiderlings, as a (protective?) cover, under which regular, small, prey catching lampshades are made. Sheet webs are the primary prey catching construct in both *Austrochilus* (Forster et al., 1987) and *Ectatosticta* (Li and Zhu, 1984). Parsimony dictates that the lampshade web of *Hypochilus* is autapomorphic and that ancestral hypochilids constructed only a sheet web. By constructing aerial webs in vegetation as does *Austrochilus* (personal obs.), they may have been primitively more arboreal and less restricted to rock habitat than they are today. Such a scenario lends further weight to the contention of a transcontinental common ancestor.

The conductor apex synapomorphy (figs. 22–25) is evidence that the Sierra Nevada

group comprising *H. petrunkevitchi*, *H. bernardino*, and *H. kastoni* does form a monophyletic clade. Restriction of the Californian forests to the coast and mountains during the Pliocene as the climate became progressively more xeric (Raven and Axelrod, 1978) may have been the initial vicariance event responsible for isolating the parent populations. The mountain corridor (the San Gabriel and Tehachapi Mountains) connecting the San Bernardino Mountains with the southern Sierra Nevada, might, as late as the humid Pleistocene, have provided gene flow between *H. petrunkevitchi* and *H. bernardino* populations, although today it may be too dry (W. Icenogle, personal commun.). Precipitation occurs mainly during the winter months with an annual range of 25–102 cm (Oakeshott, 1971). Alternatively, the isolation of *H. bernardino* could have occurred earlier due to the formation of the Mojave Desert, which is thought to have formed as early as the Oligocene as a result of movements of the San Andreas fault (Norris and Webb, 1976). *H. kastoni* is known from only two localities in northern California, the Klamath Mountains to the west [an area of high precipitation, 100–203 cm per year (Oakeshott, 1971)], and the Mount Shasta region of the Cascade Range. Volcanic activity may have played major roles in fragmenting *H. kastoni* populations in this young Quaternary range.

The *H. bonneti* lineage may have become isolated from *H. jemez* during the Cretaceous as a result of the orogeny of the Rocky Mountains. Alternatively, the separation may have occurred much more recently during the Pliocene, resembling the scenario proposed by Lowe (1950) to account for the isolation of the salamander *Aneides hardii* in the Sacramento Mountains of New Mexico. During the Pliocene, this and adjacent ranges became fragmented into “islands” of Arcto-Tertiary forest surrounded at lower elevations by Madro-Tertiary flora. Restriction of both species to refugia would have ameliorated the worst of the arid environment as the temperate forest habitat was eliminated. Certainly their contemporary distribution is congruent with such a hypothesis.

The eastern clade is clearly monophyletic and supported by several unreversed synapo-

morphies (fig. 44). The five allopatric species occupy broadly similar habitat in an area ranging from northern Alabama northeast to West Virginia (fig. 35). The northeast limit of their distribution up the Appalachian chain may have been delimited by the southern expansion of the Laurentide Ice sheet 18,000 years ago (Delcourt and Delcourt, 1981), and maintained by the low vagility of these spiders. The putative speciation events of *H. sheari* and *H. coylei* from a common ancestor have been discussed by Huff and Coyle (1992), who proposed isolation of demes by stream capture. The observed allopatric/parapatric distribution of the five species within the southern Appalachians requires some explanation in light of the hypothesized relationships. These putative relationships are difficult to reconcile with the modern distributions of the eastern clade (fig. 35). Such patterns may be a reflection of Pleistocene events which provided the opportunity for expansion of ranges during the cooler, wetter glacial maxima, and subsequent restriction to a more moist microhabitat during the warmer, drier interglacials. Such climatic changes have occurred at least three times in the southern Appalachians during the Pleistocene (Barr, 1968). The sister species *H. coylei* and *H. sheari* are confined to a small area of western North Carolina; surrounding them to the north, west, and south in a broad semicircle is *H. pococki*. *H. thorelli* is removed to the east, while *H. gertschi* abuts *H. pococki*'s range to the north. It seems likely that *H. thorelli*'s distribution was at some time more extensive to the east, thus allowing local vicariance events to isolate the parent stock of *H. coylei* and *H. sheari* from that of *H. thorelli*. Subsequent to this event *H. pococki* would have expanded into its present range.

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